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Collaborative Research and Data-Limited Assessment of Small-Scale Trap Fisheries in the Santa Barbara Channel

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Environmental Science and Management

by

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ABSTRACT

Collaborative Research and Data-Limited Assessment of Small-Scale Trap Fisheries in the Santa Barbara Channel

by

Sean Patrick Fitzgerald

Globally, most fisheries are managed ineffectively. Model-based stock assessments that estimate biomass-based reference points work well for sustainably managing data-rich fisheries, but small-scale fisheries typically lack the data and/or resources needed to perform these assessments. These fisheries comprise the majority of fisheries worldwide, and they require alternative monitoring and assessment methods to better understand fishing's impact on targeted populations and to enhance the sustainability of fished stocks. In this dissertation, I focus on the application of alternative monitoring and assessment techniques to improve understanding and management of two invertebrate fisheries in the Santa Barbara Channel (SBC) in southern California (CA).

The first two chapters focus on the multispecies southern CA rock crab fishery, which experienced rapid growth from 2010 to 2015 in the SBC. However, rock crab stock health has never been assessed because substantial biological data limitations exist, species-specific catch data is often unreported, and effort data is not available in this fishery. In the first chapter, I performed five data-limited assessments in an effort to

identify any early warning signs of depletion in the fishery. Methods selection was supported by novel decision support software (FishPath) designed to facilitate the selection of context-appropriate assessment and management options for coastal fisheries. Expert opinion of stakeholders was vital when interpreting the suite of assessment results, which suggested that the rock crab fishery may be experiencing serial depletion, effort creep, and regional overfishing. The approach taken delivers a widely applicable means for improving understanding of fishery impacts in data limited circumstances, and I suggest a proactive management strategy to address warning signs of overfishing for southern CA rock crab.

In chapter two, I employed a collaborative approach to further assess these early warning signs of overfishing. The rock crab fishery is managed as one assemblage despite life history differences across species and space, as well as spatial variation in fishing effort and species composition of the catch. Uniformly managing such a complex system renders it difficult to assess which rock crab stocks are most affected by the increased fishing pressure in the SBC. I tested for stock-specific declines by replicating a 2008 study in 2016-17, where local fishers collected key fishery-dependent indicator data across the SBC and I compared indicator values between studies. Spatially explicit multiple regression analyses revealed significant declines in male crab sizes, overall CPUE, and the proportion of crab retained (versus discarded) for all heavily targeted stocks. Evidence of decline varied with species, location, and sex, but overall, fishers caught fewer pounds of crab per trap in 2016-17 than in 2008. This work provides a foundation for an adaptive, spatially explicit, empirical management strategy for southern CA rock crab, which may help fishers to avoid financial loss and further depletion of

certain stocks. It also demonstrates that relatively simple collaborative approaches can provide valuable insight into complex fishery systems in need of improved management.

In chapter three, I focus on the use of no-take marine reserves as a tool for fisheries management. Marine reserves are a widely used and successful strategy for conserving biodiversity, but their ability to benefit adjacent fisheries through spillover of larvae, juveniles, and adults is often uncertain. Assessing fishery-related benefits of individual reserves requires careful evaluation on a case-by-case basis. This chapter examines spillover contributions from a no-take marine reserve network established in 2003 at the Northern Channel Islands, CA to the southern CA spiny lobster (*Panulirus interruptus*) fishery. Collaborative fisheries research (CFR) in 2006-08 found considerable population increases within these reserves and potential spillover across reserve borders. I replicated the 2006-08 effort in two reserves in 2018 to quantify further accumulation of biomass inside the reserves, and to test whether spillover led to increased trap yield outside reserve borders following 15 years of reserve protection. The study design controlled for individual reserve characteristics, fisher behavior, and environmental conditions. I found that catch per trap increased 125–465% deep within reserves, 223–331% near outer reserve boundaries, and did not increase at control sites. Spillover therefore contributes to enhanced catch for the Southern CA spiny lobster fishery, and this study illustrates the utility of CFR for assessing the effectiveness of marine reserves as fishery management tools worldwide.

As a whole, this dissertation exemplifies the use of collaborative, alternative approaches to stock monitoring and assessment that can be applied to improve the management of small-scale fisheries worldwide.

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I. Detecting a need for improved management in a data-limited crab fishery

Abstract

A majority of fisheries worldwide lack effective management because of poor quality data and limited resources. Data-limited stock assessments are increasingly used where model-based, data-rich approaches are not possible. Yet, their widespread use is constrained by several important limitations, especially the inability to estimate biomass or maximum sustainable yield (MSY)-based reference points. Here we applied several data-limited stock assessments and utilized expert opinion to identify early warning signs of depletion in the rapidly growing Southern California (CA) rock crab fishery, a small scale yet economically valuable fishery being managed with relatively limited information. We chose our specific assessment methods with the aid of a decision support tool (FishPath) designed to help identify context-appropriate options for assessing and managing fisheries. Results of five assessments indicated that serial depletion, regional overfishing, and effort creep may be occurring in the rock crab fishery. Expert opinion regarding changes in fishery operations and fishing effort provided vital insights for interpreting assessment results. We illustrate a general path for enhancing understanding of fishery impacts in a data limited fishery, and sound rationale for proactive management to address warning signs of overfishing in the southern CA rock crab fishery.

1. Introduction

Conventional stock assessments estimate maximum sustainable yield (MSY)-based reference points for management by fitting a population model to a time series of fishery-dependent and -independent data (Carruthers et al., 2016, Dowling et al., 2016). Fisheries managed using conventional stock assessments are, with a few exceptions, large-scale, data-rich, and relatively well-managed (Hilborn & Ovando, 2014). Such characteristics describe about 10% of global fisheries, while 90% of the world's fisheries are small-scale and lack the data and resources needed to perform conventional stock assessments (Costello et al., 2012, Worm & Branch, 2012, Carruthers et al., 2014, FAO, 2016). Poor management of these data-limited fisheries threatens hundreds of millions of people who rely on sustainable fisheries for protein intake and employment (FAO, 2016).

Relatively simple quantitative and sometimes qualitative assessments can help in data-limited situations by elucidating trends in catch, effort, or proxy indicators of stock status, without quantifying traditional biomass-based reference points (Kruse et al., 2005, Dowling et al., 2015, Quinn et al., 2016). Simulations indicate that data-limited assessments can lead to better management results than conventional, data-rich methods when paired with context-specific monitoring and decision rule protocols (Geromont & Butterworth, 2015, Carruthers et al., 2016). However, data-limited methods can also lead to poor management outcomes, especially when using inadequate data or relying on an inappropriate type of assessment (e.g., Carruthers et al., 2014, Free et al., 2017). Applying multiple data-limited assessments that use a variety of data streams may be more suitable than selecting a single assessment type that may not be appropriate, or the results of which demonstrate even moderate uncertainty (Carruthers et al., 2014, Berkson

& Thorson, 2015). For example, Carruthers et al. (2014) demonstrated poor performance of assessments that used catch data only, but stressed the high value of adding information about historical fishing effort or depletion levels to improve assessment performance.

The use of several independent yet complementary methods may improve the ability to make informed decisions under certain circumstances. For example, Lindegren et al. (2012) suggested that multiple methods be used to diagnose early warning signs of ecological regime shifts because ecosystems are unique, the performance of individual diagnostic tools are context-dependent, and a suite of results provides the most robust information. Using multiple data-limited assessments is realistic for many fisheries because these methods are often designed to be easily understood and implemented in diverse socioeconomic and governance settings, usually require few resources, and are emerging as pre-packaged, management-focused computer applications (Dowling et al., 2016). Consideration of multiple assessment outputs and the patterns they suggest may serve as a means to direct management guidance in a proactive manner (Prince et al., 2011).

Selecting the appropriate assessments from the wide variety of available data-limited methods is often a challenging and subjective process (Dowling et al., 2016). Navigating the universe of options can be daunting without an understanding of the available methods, including input requirements and associated caveats and assumptions. FishPath – a newly developed decision support platform designed to facilitate the selection of appropriate assessment and management approaches for data-limited fisheries – can help users identify those methods that are right for their fishery (Dowling et al., 2016). The

FishPath tool (Dowling et al. 2016) is a repository of information that catalogues data requirements and assumptions of more than 50 assessment methods to help users identify an appropriate assessment methodology for use. The tool does not provide advice, nor does it perform assessments. Rather, it serves as an organizational framework to streamline the process of selecting appropriate methods. We used FishPath to identify a select set of data limited assessment approaches for the rapidly growing Southern California (CA) multispecies rock crab fishery in the United States (US). We applied these methods to aid stakeholders and managers in understanding the impacts of fishing on the resource and to begin the process of developing management guidance.

Our primary objective was to explore whether data-limited rock crab stocks in southern CA are threatened with overfishing. Studies of crab and other fisheries have focused on detecting overfishing, but the methods developed to date have largely been data-rich or model-based (Myers & Quinn, 2002, Orensanz et al., 2005). Here, we systematically selected an array of data-limited assessments, applied them to data streams already collected by the state, and identified early warning signs of overfishing in the previously unassessed multispecies CA rock crab fishery. The process identified here and the results of this work provide managers and stakeholders with a foundation for being proactive in the face of uncertainty without a need for technical and resource intensive assessment approaches. We do not suggest that data-limited assessment should immediately translate into regulatory action, rather that our process stimulates informed decision making regarding how to monitor, assess, and manage a fishery. The guiding principles of fishery management law at US state and federal levels call for such approaches, dictating that management be based on the best available scientific

information, and that action should not be significantly delayed by lack of information or high levels of uncertainty (CDFW, 2001, MSFCMA, 2007). We encourage similar processes be undertaken for small-scale data-limited fisheries worldwide.

2. Methods

2.1 Study system: Southern CA rock crab

The Southern CA rock crab fishery targets male and female red (*Metacarcinus* or *Cancer productus*), yellow (*Metacarcinus* (formerly *C.*) *anthonyi*), and brown (*Romaleon antennarium* (formerly *C. antennarius*)) rock crab. The fishery primarily operates within the Santa Barbara Channel (SBC) coastal marine ecosystem, which covers an area of several thousand square kilometers and includes coastal stretches of mainland CA and the Northern Channel Islands (Fig. 1). Small-scale, state-managed fisheries like rock crab often operate without harvest control rules that adjust catch or effort in response to assessment outputs (Larinto, 2013). The CA Department of Fish and Wildlife (CDFW) oversees all aspects of management for CA rock crab including permitting, enforcement, and recommendations for decision makers. CDFW manages rock crab by restricting the number of available southern CA permits and enforcing a statewide size limit of 108 mm. However, rock crab growth rates and maximum sizes vary with species, sex, and location, so the size limit is of unknown efficacy for each individual species and there is no other catch or effort restriction for permit holders (Carroll & Winn, 1989, Culver et al., 2010). Mating and molting cycles, recruitment, and life history traits of rock crab are also poorly understood, especially as they vary across the steep gradient of marine productivity in the SBC (Wilson et al., 2012).

The CA rock crab fishery is subjected to data collection protocols, but not at levels sufficient to generate information that can inform estimates of biomass or MSY. Consequently, the fishery has never been assessed, rapid fishery growth in recent years has created the potential for overfishing, and the fishery is managed via a single size limit despite being multispecies and spatially structured (Parker, 2003, Culver et al., 2010). Many crab fisheries worldwide, both data-poor and data-rich, have suffered from overcapacity and serial depletion when managed under size, season, and sex-based methods, despite comprising a multibillion dollar annual global industry (Orensanz et al., 1998, Fina, 2005, Salomon, 2007, FAO, 2016). Notoriously large uncertainties surround model-based estimates of biomass or MSY for many crab fisheries - even with robust data - because of difficulties in aging individuals, variable incremental growth patterns, strong spatial population structure, and pervasive environmental influences on model parameters, including estimates of recruitment and natural mortality rates (Orensanz & Jamieson, 1998, Zheng, 2005, Punt et al., 2013, Szuwalski et al., 2015). Our application of data limited assessments to detect signs of overfishing without estimating MSY aims to provide a suitable foundation for management that may be beneficial to CA rock crab and other data limited crab fisheries worldwide.

The only long-term data for the CA rock crab fishery are commercial landing receipts that collect total landings by 10 sq. nm “blocks”. Landings receipts do not provide effort data and did not distinguish between species until 1995, and the majority of catch for all three species was still recorded as a single category called “unspecified rock crab” until 2010 (Parker, 2003, CDFW, 2015). Rules adopted in 2004 capped the number of southern rock crab trap permits and provided no mechanism for entry of new participants.

Rule changes in 2010 then allowed transfer (sale) of permits at a rate of five per year. Signs of a related increase in fishing intensity included a near doubling of landings from 2010 to 2014, with over 2,000 metric tons (MT) of rock crab sold for $6.845 million USD in 2014-15 (CDFW, 2015). The fishery then closed in November of 2015 due to a domoic acid outbreak. The closure lasted two months along the mainland SBC coast and five months for most of the Channel Islands, which affected fishing effort to an unquantified degree (CDFW, 2016). Some fishers in interviews reported seeing smaller and fewer crab in their traps than in past decades, and unpublished data showed that catch rates and crab sizes were lower in fished areas than in adjacent Santa Monica Bay, where commercial crabbing had been disallowed for decades (Parker, 2003, personal communication). We compiled all existing information on the rock crab fishery (Table S1) by interviewing fishers, scientists, and managers, reviewing available literature, and organizing landing receipt data from 1970-2015 (CDFW, 2015). We focused on the period of 1970-2015 to avoid the confounding impact of the fishery closure, but we also obtained a summary of total landings in 2016 and preliminary total landings in 2017 (CDFW, 2017). We used four types of data in our analyses: total landings, spatial distribution of catch, and species composition of catch (from landing receipts) as well as expert opinion regarding market demand and fishery operational characteristics.

2.2 Data-limited assessment of CA rock crab

We identified and performed five data-limited assessments to detect early warning signs of overfishing in the CA rock crab fishery after considering over 40 published methods (Dowling et al., 2016). These five methods (and > 40 others) are catalogued in FishPath with their associated data requirements, limitations and assumptions. FishPath is

designed to help stakeholders and managers identify potential assessment options for their fishery, but does not execute or recommend any particular method (Dowling et al. 2016). The decision of which assessments to ultimately perform lies entirely with the stakeholders, managers, and/or scientists using the software and requires independent expertise to carry out these analyses. Here, we performed a thorough review of the required inputs, limitations, caveats, and uncertainties associated with each method in the published scientific literature and in FishPath, respectively. We then chose each assessment after careful consideration of fishery data availability and a requirement not to violate assumptions within each model. Meetings and interviews with fishers, managers, and scientists were an integral part of our final methods selection and the interpretation of our results. Details of applying each assessment to rock crab are provided below. Unless otherwise noted, all our analyses were performed in R (R Core Team, 2016).

2.2.1 Productivity Susceptibility Analysis (PSA)

Understanding vulnerability of a stock to overfishing is an important responsibility of a fishery manager. Productivity Susceptibility Analysis (PSA) uses basic life history information and fishery operational characteristics to determine how vulnerable stocks are to overfishing, and has been used to assess overfishing risks in case studies across the globe (Cope et al., 2011, Hobday et al., 2011, Zhou et al., 2016). Following the PSA protocol from Patrick et al. (2009), productivity and susceptibility of each rock crab species were scored from 1 (low) to 3 (high) and vulnerability was calculated from 0-3 for each species using the NOAA Fisheries Toolbox (NFT, 2010). Productivity scores are based on life history traits, which we derived through a combination of expert judgment, published growth rates, longevity estimates, and fecundity information for rock crab, or

literature searches for other crab species (Table S1, S2). The life history parameters used to score productivity include intrinsic growth rate (r), maximum age, the von Bertalanffy growth coefficient (K), natural mortality rate (M), fecundity, and age at maturity. Our estimates satisfied PSA guidelines for scoring each species of rock crab on a 1-3 scale, despite parameter uncertainty and spatial variability (Shields, 1991, Yamada & Groth, 2016). Susceptibility scores are based on each species' catchability, as well as fishery management characteristics (e.g. whether catch limits or protected areas exist), which we largely derived through dialogue with fishers and managers. Two unobtainable values (fishing rate relative to M and spawning biomass) were unscored and not used following Patrick et al. (2009).

We also explored sensitivity in rock crab vulnerability estimates by generating two new sets of productivity and susceptibility scores. The first set contained lower productivity and higher susceptibility scores than we assigned to any actual rock crab species, representing a "worst-case" scenario for vulnerability, and the second set represented a "best-case" scenario (i.e., higher productivity and lower susceptibility than actual rock crab scores). We chose parameter values either by selecting the most extreme values for any species in the published literature (Table S1), or by using expert opinion to determine a parameter's most extreme conceivable value. We also scored the unobtainable parameters as a 3 in the conservative (worst-case) scenario, but left them unscored in the optimistic (best-case) scenario. There is no knowledge of spawning biomass or fishing rate for CA rock crab, but other studies suggest a score of 3 is feasible for heavily targeted crab fisheries (e.g. Lipcius & Stockhausen, 2002, Windsland, 2014). We attempted to estimate values that were viable for actual rock crab populations in the

SBC with these scenarios, but high levels of uncertainty for some parameters means that these scores do not necessarily represent upper and lower limits of true vulnerability scores for CA rock crab. An indication of the underlying uncertainty in PSA is provided in an associated data quality index (DQI), where the belief in each score is scored on a scale from 1 ("best data") to 5 ("no data") according to the criteria in Table 4 of Patrick et al. (2009). The DQI is then a weighted average of each score. DQI scores above 3.5 are considered low data quality, whereas scores below 2.0 are considered high data quality. We calculated the DQI score for each rock crab species, but not for the two sensitivity estimates. Unscored parameters received a score of 5 and are reflected in the overall DQI score in accordance with Patrick et al. (2009).

2.2.2 Changes in spatial distribution of catch

Overfishing can occur even if overall fishery catch is consistently high over time. Analyzing the spatiotemporal distribution of fishery landings reveals patterns that can reflect localized overfishing and serial depletion (Orensanz et al., 1998, Walters & Bonfill, 1999). We obtained port-level data from 1970-2015 from CDFW (2015) and separated rock crab landings by port to perform a long-term spatiotemporal analysis of fishery-wide catch patterns. We separated 14 ports into three port "complexes" based on locations that together account for over 95% of the fishery's historical catch: the "northern ports complex" (2 ports, consisting of 14.5% of total historical catch), the "SBC complex" (3 ports, 48.4%), and the "southern ports complex" (9 ports, 32.2%; Fig. 1, Table S3). We visualized landings by port complex from 1970-2015 to examine whether large-scale spatial shifts in CA rock crab landings have occurred over time.

In addition to port-level data, commercial landing receipts include the 10x10 nm fishing block where landed specimens were caught. Block-level data prior to 1996 were deemed unreliable due to faulty reporting (e.g., nonsensical fishing block numbers), so we used fishing block landings data from 1996-2015 to assess spatiotemporal changes in four regions: the southern mainland coast (from the CA-Mexico border to Santa Monica), the SBC mainland coast (Santa Monica to Point Conception), the Northern Channel Islands, and all remaining fishing blocks (block-level reporting was unreliable in ports north of the SBC). Fishers rarely moved between these areas, each of which has unique biological and environmental characteristics (Harms & Winant, 1998, Dong et al., 2009, Culver et al., 2010, personal communication). We quantified spatial shifts in fishery catch by calculating percentage change in landings by region in 5-yr increments.

2.2.3 Cumulative Sum (CUSUM) Control Charts

CUSUM analysis is a statistical quality-control method used to identify persistent deviations from a mean in an observed process (Hawkins & Olwell, 1998). Scandol (2003) first suggested its use in fisheries as a means of quantifying variation in a time series of catch data. CUSUM has since been employed in numerous case studies to assess fishery performance across multiple stock status indicators (Mesnil & Petitgas, 2009, Petitgas, 2009) and has been tested as a means to directly inform harvest control rules (Pazhayamadom et al., 2013, 2015, 2016). CUSUM, in isolation, is not appropriate to inform management actions directly when using a single indicator (Scandol, 2003, Petitgas, 2009, Pazhayamadom et al., 2015, 2016). Therefore, in this study we used CUSUM to detect whether patterns in CA rock crab catch data reflect warning signs of regional overfishing that warrant further attention by management. We generated

CUSUM control charts separately in four regions: (1) all of CA, (2) southern ports, (3) northern ports, and (4) the SBC (see Fig. 1). Comparing results from localized versus statewide analyses addressed whether aggregating the data masked important spatial trends in rock crab catch over time. The first three analyses extend from 1970-2015 to identify chronic trends in catch levels compared to the fishery's initial state in the 1970s. The SBC analysis extends from 1996-2015 because the SBC was minimally fished until the 1990s, and the primary objective in this region was to explore the impacts of the post-2010 effort increase (D. Pazhayamadom, personal communication). Extending the SBC analysis to 1970-2015 did not significantly alter our results.

CUSUM analysis consists of calculating the cumulative sum of deviations of an indicator (C_t) away from a control mean ($\bar{X}$). $\bar{X}$ is often the average value of a fishery-related metric taken from a scientific study or a stable historical reference ("control") period (Scandol, 2003, Mesnil & Petitgas, 2009). Each observation (C_t) in the time series is then standardized according to the equation

$$Z_t = (C_t - \bar{X})/\mathrm{sd}(\bar{\sigma}), \quad \text{(Eq. 2.1)}$$

where $\bar{\sigma}$ is the control standard deviation, and the deviations of Z_t from $\bar{X}$ are in units of $\bar{\sigma}$. The upper (θ^+) and lower (θ^-) CUSUMs of the deviations are computed separately where

$$\theta_0^+ = 0 \text{ and } \theta_0^- = 0,$$

$$\theta_t^+ = \max[0,\ \theta_{t-1}^+ + Z_t - k],$$

and

$$\theta_t^- = \min[0,\ \theta_{t-1}^- + Z_t + k]. \quad \text{(Eq. 2.2)}$$

The *k* parameter is the allowance that defines how much variability is accepted as background noise. That is, when $|Z_t| < |k|$ in a given year, the observation decreases $|\theta^+|$ or $|\theta^-|$ to a minimum of zero. When $|Z_t| > |k|$, θ^+ increases if Z_t is positive and θ^- decreases if Z_t is negative (Scandol, 2003, Mesnil & Petitgas, 2009). The observed process is said to be "in-control" if θ^+ and θ^- remain within an acceptable decision interval (defined as $\pm h$) and "out-of-control if θ^+ or θ^- accumulates to exceed $\pm h$ in a given year (Hawkins & Olwell, 1998, Mesnil & Petitgas, 2009). CUSUM control charts visualize persistent trends in measured indicators relative to the initial reference period by plotting θ^+ and θ^- values over time as they relate to the bounds defined by *h*.

The user defines $\bar{X}$ (and $\bar{\sigma}$), *h*, and *k* in CUSUM analysis. $\bar{X}$ and $\bar{\sigma}$ are ideally known to reflect sustainable parameter values calculated through scientific study or by monitoring indicators during a historical period of acknowledged fishery sustainability (Scandol, 2003, Mesnil & Petitgas, 2009). In these cases, out-of-control signals can represent unsustainable fishing levels and can even inform managerial decision rules (e.g. Pazhayamadom et al., 2015, 2016). However, sustainable parameter values are incalculable for CA rock crab, despite having a significant number of catch-based data points for CUSUM analysis. In the absence of a sustainable reference period, we followed Scandol (2005), Mesnil & Petitgas (2009), and Petitgas (2009) to define $\bar{X}$ and $\bar{\sigma}$ as the mean catch and standard deviation of the first ten years of data for each analysis. Shortening the number of data points and using the beginning of the time series as the control period reduces the probability of user bias (D. Pazhayamadom, personal communication) and is consistent with our objective to detect deviations relative to each

stock's initial state rather than to claim whether fishing is above or below sustainable levels.

We used (h, k) = (3, 0.5) in all analyses. Pazhayamadom et al. (2013) recommends k = 0.5 for short-lived species, which showed better performance and sensitivity compared to when k = 1.5. Smaller k values are more precautionary, and are thus better suited for trend detection and prioritizing future management needs than larger k values, which increase the risk of failing to notice important changes (Pazhayamadom et al., 2015). Pazhayamadom et al. (2013) use h = 1, but we adjusted h to equal 3 because Scandol (2003) recommends using a higher h value when standardizing data based on a subset of a historical period rather than the entire time series. Scandol (2003) also showed that when k = 0.5, h values of approximately 3 yielded optimal CUSUM performance when dealing with fairly short-lived species and high variance in time series catch data, as is the case for CA rock crab. We explored values from (h, k) = (0, 0) to (h, k) = (3, 1.5) in sensitivity analyses, covering the range used in most fishery-related CUSUM applications, and found little impact on results other than altered extremity of θ^+ and θ^-.

2.2.4 Changes in species composition

Changes in species composition may indicate overfishing of one or more species in multispecies fisheries (Jin & Tang, 1996, Collie et al., 1997, Dowling et al., 2008). Particularly for a fishery like CA rock crab, where each species is spatially segregated due to different environmental requirements, intense exploitation of one type of fishing ground may disproportionately impact the species found in a given area. We analyzed species composition of landed catch separately for the Northern Channel Islands and along the mainland CA coast to quantify spatially-specific changes. Historically, yellow

rock crab constitutes the majority of catch along the coast, and nearly all offshore catch at the islands consists of red and brown rock crab (CDFW, 2015). Fishers in interviews stated that all three rock crab species are highly marketable and fetch a similar price per pound, so fluctuating market demand is unlikely to cause species composition changes. We limited analyses to 2008-2015 because nearly all landings were reported as "unspecified rock crab" prior to 2008. Many landings remained unspecified after 2008, so we also determined which individual 10x10 nm fishing blocks had consistent species-level reporting (defined as < 10% unspecified rock crab). We analyzed species composition changes separately in these individual blocks in an attempt to filter out fishers who did not reliably record species. We followed the "rule of threes" for every analysis, meaning we only present results if we used data from at least three fishers.

2.2.5 Changes in fishery catch by permit type (latent effort creep analysis)

Latent effort creep has rendered management efforts ineffective and led to overfishing in case studies around the world (Kompas et al., 2009, Teh et al., 2017). An important issue for the CA rock crab fishery is whether latent effort creep of permit transfer recipients caused the explosive increase in rock crab landings after 2010. We compared the percentage of total catch landed by the new permit holders (permittees) from 2011-2015 versus those same permits with different owners (transferees) from 2006-2010 to quantify the relative contribution of new permittees. We also calculated landed catch separately from 2006-2010 and 2011-2015 for existing permit holders who were not involved in the permit transfer process, and compared this to the permittees and transferees to determine how much each group contributed to the recent landings spike. We do not have permit-specific data after 2015, but we acquired a summary of total rock

crab landings for the next two years (CDFW, 2017) and explored whether catch continued to increase fishery-wide in 2016-2017.

3. Results

3.1 Data-limited Assessment of Southern California Rock Crab

The suite of data-limited assessments performed for the CA rock crab fishery generated four main results: (1) CA rock crab stocks are not particularly vulnerable to overfishing (section 3.1.1), (2) the spatial distribution of CA rock crab catch changed through time in a manner consistent with serial depletion (sections 3.1.2 and 3.1.3), (3) the reported species composition of CA rock crab catch changed from 2008-2015, most notably in the final two years of recorded data (section 3.1.4), and (4) substantial latent effort creep occurred in the CA rock crab fishery from 2011-2015, but new permittees and existing permit holders added equally to increased catch levels after 2010 (section 3.1.5). Essential details from each result are as follows.

3.1.1 Productivity Susceptibility Analysis (PSA)

PSA indicated that all three species of rock crab are moderately to highly productive (scores ranged from 2.40 to 2.55) but are similarly susceptible to fishing pressure (2.17 for all three species), resulting in vulnerability scores ranging from 1.25 to 1.31 (Fig. 2). Vulnerability scores for the "best-case" and "worst-case" scenarios were 1.15 and 1.87, with moderate to high scores for both susceptibility (2.11 and 2.67) and productivity (2.70 and 2.15; Fig. 2). Guidelines from Patrick et al. (2009) and Cope et al. (2011) suggest that vulnerability scores below 1.8 suggest low risk of being overfished, so all PSA results for rock crab indicated a low risk of overfishing with the exception of the conservative scenario that estimated moderate vulnerability. However, the DQI scores for

red, brown, and yellow rock crab were 2.75, 2.95, and 3.1 respectively, so data quality is relatively low. Results are therefore uncertain and should be treated with caution.

3.1.2 Changes in spatial distribution of catch

Port-level analysis of landings data from 1970-2015 revealed dramatically reduced catch levels in southern ports from the early 1990s to 2015 (Fig. 3). Catch in northern ports experienced a similar decline beginning in the late 1990s. By contrast, the SBC experienced steadily rising catch beginning in the late 1980s, with a substantial increase after 2010 (CDFW, 2015). The slight decrease in landings from 2014 to 2015 was likely due to the domoic acid-induced fishery closure in the final two months of 2015 (McCabe et al., 2016). Block-level analysis also revealed a change in the location of rock crab landings over time, highlighted by a rapid and dramatic expansion of fishing effort at the Channel Islands over the past 20 years (Fig. 4). Values are inexact due to extensive misreporting of block numbers by fishers and buyers, but reported landings between the five-year periods of 1996-2000 and 2011-2015 increased by 263% at the islands, 83% along the SBC coast, and just 27% along the Southern CA coast. Landings decreased by 60% in all other fishing grounds. The islands accounted for 33% of fishery-wide landings from 2006-2010, 47% from 2011-2015, and 63% of landings in 2015 (CDFW, 2015).

3.1.3 Cumulative Sum (CUSUM) Control Charts

CUSUM analysis showed that statewide rock crab landings increased dramatically starting in the 1980s compared with the reference period of 1970-1979, and that positive deviations accumulated fastest during the 1980s and after 2010 (Fig. 5a). Analysis of the SBC showed a similar trend of consistently increased landings following the reference period of 1996-2005, as the upper catch CUSUM (θ^{+}) continued to increase through 2015

(Fig. 5b). Analyses for the southern and northern ports, however, yielded entirely different results. In the southern ports, θ^+ rose to out-of-control levels in 1985 but declined to zero by 1996, and the lower catch CUSUM (θ^-) reached out-of-control levels by 1994. Negative deviations continued to accumulate through 2015 (Fig. 5c), meaning catch levels in southern ports during the 1980s were substantially higher than the 1970-1979 average (control mean), but catch levels were below the control mean in every year since the early 1990s. Northern ports showed a similar pattern a few years later. Extreme positive deviations (out-of-control θ^+) accumulated in the 1990s, followed by negative deviations (θ^-) reaching out-of-control levels by 2008 and continuing through 2015 (Fig. 5d). Again, this means catch levels in northern ports were consistently higher during the late 1980s and 1990s than during the control period (1970-1979), but were below the control mean in every year since 1999.

In summary, landings rose to historically high levels in the 1980s-90s then crashed without recovering in both the southern and northern port complexes. Landings then dramatically rose in the SBC complex starting in 2010, and although there were not yet signs of a crash in 2015, statewide rock crab landings data from 2016 and 2017 showed that landings in the SBC have begun to substantially decrease (see section 3.1.5). Aggregated statewide analysis failed to detect severely reduced landings for any region or time period.

3.1.4 Changes in species composition

Recorded species composition changed substantially from 2008-2015 (Fig. 6). Red and brown rock crab catch notably increased fishery-wide in recent years (Fig. 6a), but the prevalence of unspecified rock crab renders it difficult to quantify how much more

red or brown rock crab fishers actually landed versus how much of the increase was a byproduct of better reporting (Fig. 6a-c). At the Northern Channel Islands, where red and brown rock crab are the dominant species, landings more than tripled from 2008-2015 and a higher proportion of brown rock crab was reported in 2014-2015 for the region as a whole (Fig. 6b). Catch levels were more stable from 2008-2014 along the SBC mainland coast but dropped precipitously in 2015, and a much lower proportion of yellow rock crab was reported in 2014-15 (Fig. 6c). Fishers in individual fishing blocks 656 and 653 along the coast (Fig. 6d) recorded over 94% of their catch to the species-specific level since 2008 (except in 2012), and landings in these blocks revealed a substantial decline in the proportion of yellow rock crab from 2013-15 (Fig. 6e-f). During this time, these two blocks accounted for over one-third of the total catch along the SBC mainland coast, and the percentage of reported yellow rock crab in the catch decreased from 94% to 40% in block 656 and from 90% to 61% in block 653. The two coastal blocks with the next highest landings, 654 and 665, had high proportions of unspecified rock crab until 2014 and are not shown, but the proportion of yellow rock crab in these blocks decreased by 13-21% from 2014 to 2015 (CDFW, 2015).

3.1.5 Changes in fishery catch by permit type (latent effort creep analysis)

The addition of more fishers via permit transfers activated substantial latent effort in the CA rock crab fishery. New permittees landed 976 MT of rock crab accounting for 21.4% of the total catch from 2011-2015, whereas the previous owners of those permits (transferees) landed just 177 MT of rock crab accounting for 6.26% of the total catch from 2006-2010. New permittees therefore caught 799 MT more crab from 2011-2015 than transferees did from 2006-2010. However, existing permit holders that were not

involved in the transfer process increased their catch by 804 MT over the same time period. These fishers landed 2,644 MT of rock crab from 2006-2010 and 3,448 MT from 2011-2015, reflecting increased effort of both existing and new permit holders (CDFW, 2015; Fig. 7). Therefore, latent effort creep considerably contributed to increased landings of CA rock crab, but it does not fully explain the dramatic rise in catch after 2010. Fishers in interviews said market demand for rock crab reached unprecedented levels in recent years, offering an alternative explanation for intensified effort. Despite continued high market demand, fishery-wide catch in 2016-2017 alarmingly fell by 43.5% compared to 2014-2015. All fishing grounds were open and unaffected by domoic acid in 2017, yet preliminary data shows catch was 45.9% lower in 2017 (580 MT) than in 2014 (1,073 MT; CDFW, 2017).

4. Discussion

Results from multiple data-limited assessments revealed symptoms of serial depletion, whereby individual rock crab populations appeared to be sequentially overexploited across space and time. Rock crab catch levels in ports south of the SBC peaked in the 1980s then dramatically declined to historically low levels in the 1990s. The same pattern then emerged in ports north of the SBC in the 1990s and 2000s, and in 2014 landings peaked in the SBC itself (Figs. 3 and 5). Catch has now begun to dramatically decline in the SBC as well. Landings for the entire state of CA in 2016-2017 fell to just 71.3% of what was caught in the SBC alone in 2014-2015 (CDFW, 2015, 2017). The SBC also experienced a notable spatial shift in catch distribution towards the offshore Northern Channel Islands over the past two decades (Fig. 4). This sequential rise-peak-demise pattern in catch across regions and geographic expansion to more

distant ports and offshore locations are hallmark signs of serial depletion for crustaceans (Orensanz et al., 1998). Changes in species composition exhibited additional signs of a depleted stock. Catch of the most commonly targeted species along the coast (yellow rock crab) recently declined (Fig. 6), and overfishing typically affects the dominant species first (Jin & Tang, 1996, Collie et al., 1997). Additionally, fishers revealed that there have been no recent changes in species-specific marketability for rock crab, and vessel and gear types remained similar throughout the history of the CA rock crab fishery, so these factors do not explain changes in catch or species composition. PSA analysis indicated low vulnerability of CA rock crab stocks, but collectively our analyses strongly suggested warning signs of overfishing and a need for enhanced management.

We selected and performed context-appropriate assessment methods and combined outputs into an inference-based understanding of overfishing potential in the CA rock crab fishery. This case study can serve as a model to diagnose whether targeted stocks exhibit signs of overfishing, despite an inability to generate conventional estimates of stock status. We systematically evaluated the assumptions and limitations of every potentially appropriate data-limited assessment and information stream known to us from published literature and FishPath, and selected a subset of methods based on our evaluation and expert knowledge. Using a standardized tool like FishPath helped us to avoid overlooking vital information during methods selection. For example, FishPath recognized the importance of spatially assessing and managing CA rock crab due to the species' benthic and sedentary nature (Orensanz & Jamieson, 1998, Wilson et al., 2010, Szuwalski & Punt, 2015). Finally, we chose assessments that required independent data inputs and were not all biased by the same factors. We recommend following these

guidelines and integrating FishPath or a similar tool into selection of data-limited management approaches to provide consistency and objectivity, and to ensure that all options are considered.

Failure to consider available data comprehensively in a suite of assessments could have led to incomplete or incorrect conclusions regarding CA rock crab fishery status. First, analysis of statewide catch data that ignored spatial variation failed to capture the severe declines in rock crab catch south and north of the SBC (Fig. 5). Fishery-wide catch levels of rock crab remained high over time, as is typical in cases of serial depletion, so signs of spatially-specific overfishing would have been difficult to detect in aggregated statewide analyses (Figs. 3-6, sections 3.1.2-3.1.4; Orensanz et al., 1998, Salomon et al., 2007). Second, analysis of catch data without distinguishing landings by permit type would have perpetuated the misconception that an influx of new fishers was the sole driver behind increased fishing effort after management legalized permit transferals in 2010. Substantial latent effort was activated via new permittees in the rock crab fishery from 2011-2015, but our analysis showed that existing fishers simultaneously increased their catch by a similar magnitude (Fig. 7). Stakeholder input helped determine that increased market demand likely influenced fishing effort to a similar degree as the 2010 management decision, and that demand remained extremely high through 2017. Individual fishers in interviews indicated that they have not changed fishing practices or reduced effort following the fishery closure in 2015, so the severely reduced fishery catches in 2016-2017 may serve as a warning sign of potential overexploitation. Third, one of the most widely used methods presented in this study (PSA) indicated little overfishing concern for rock crab, but these results are uncertain.

Hordyk and Carruthers (2018) suggest that the calculation of a single vulnerability score through PSA is overly simplistic and that PSA performs poorly over a wide range of conditions, questioning the validity of this approach. PSA results for rock crab may also be particularly misleading because PSA was originally designed for and applied to vertebrate fisheries, so some parameters may not be well-suited for application to crab fisheries. For example, a species receives a score of 3 (high productivity) when its maximum size is smaller than 60 cm, which is clearly an unrealistic benchmark of carapace width for any crab species and may lead to artificially inflated productivity scores. We included PSA in this study to emphasize that other crab fisheries should treat PSA results with caution, and to suggest that further research is needed to understand the suitability of PSA for invertebrate fisheries. Ultimately, these three examples illustrate the necessity of including multiple data streams and a diversity of quantitative and qualitative assessments in order to provide the most comprehensive understanding of overfishing risks.

Our results indicated early warning signs of overfishing for CA rock crab in the SBC, yet the individual data-limited assessments used in this study have substantial limitations, including an inability to formally assess uncertainty. For example, Zhou et al. (2016) showed PSA was overly precautionary in many cases, but for reasons outlined above it is unclear whether we overestimated or underestimated rock crab vulnerability. Fishing effort, catch levels, and rock crab population dynamics are also affected by numerous factors unrelated to fishing (Lipcius & Van Engel, 1990, Szuwalski et al., 2015). For example, complex environmental forcing mechanisms such as persistent oceanic fronts and mesoscale coastal eddies influence recruitment patterns in the SBC (Nishimoto et al.,

2002, Woodson et al., 2012). Recruitment rates are therefore unknown for all three rock crab species, despite being well studied for *Cancer* species in northern and southern CA (e.g. Wing et al., 1995, Botsford, 2001). Because of these limitations, it is impossible to assess with high certainty whether (1) the CA rock crab fishery can withstand the increased fishing pressure we detected at the Channel Islands, (2) specific species are overfished, or (3) serial depletion is definitively occurring. There are data quality concerns as well because fishers make inexact estimates of poundage, species, and location on landing receipts, but this uncertainty is less problematic here than in cases where data is used to calculate reference points (Yaeger et al., 2017). We minimized these concerns by restricting analyses to locations with consistent species-level reporting and by avoiding block-level analyses with nonsensical block numbers. Additionally, we examined the potential influence of environmental conditions on rock crab landings over time by performing cross-correlation analysis to determine whether a correlation exists between rock crab landings and CA ocean temperature data from the California Cooperative Oceanic Fisheries Investigation (CalCOFI, 2017). We analyzed the entire state as well as each individual port complex and found that temperature and rock crab catch were not significantly correlated on immediate or lagged timescales. The caveats and uncertainties of our analyses are still important, and understanding CA rock crab stock status would require further research. More importantly, however, our multiple method approach was designed to produce early warning signs indicating that a targeted stock may be undergoing overfishing - not as a means to produce a reliable estimate of stock status. Although we do not recommend specific management interventions for CA rock crab based on our analyses, we do encourage a proactive approach to engaging in a

management planning process to address the multiple signs of overfishing we have uncovered.

Scientists and managers dealing with small-scale fisheries must take action and make challenging decisions in uncertain conditions. Following best practices of precautionary management requires that stakeholders and managers proactively address warning signs of overfishing (CDFW, 2001, MSFCMA, 2007). Data-limited assessment approaches, such as those identified here, offer stakeholders and managers the opportunity to prevent the historical pattern of serial depletion from worsening in CA by responding to fishery changes in the absence of stock status estimates. For example, discussions between stakeholders, managers and scientists in Australia engendered the development of harvest strategies that require additional monitoring or analysis whenever the species composition of the catch changes in order to elucidate reasons behind the change (Dowling et al., 2008). In contrast, failure to detect or act upon the types of warning signs discussed in this study has led to collapsed stocks and adversely impacted communities reliant upon fishery resources across the globe (Harremoës et al., 2002). For instance, increased market demand resulted in crab fishery collapse in multiple cases (DA-BFAR, 2004, Loucks, 2007), serial depletion of benthic species is widely documented in CA and worldwide (Orensanz et al., 1998, Karpov et al., 2000, Anderson et al., 2007, Salomon et al., 2007, Miller et al., 2014), and overfishing of key species has severely impacted local ecosystems and community structure in demersal multispecies fisheries (Jin & Tang, 1996, Collie et al., 1997). We detected all three of these warning signs for CA rock crab, and we recommend action to ensure ecological and economic sustainability of the fishery.

"Action" for Southern CA rock crab stocks does not mean imposing static regulation upon fishers based solely on data-limited assessment results. Instead, our results can guide the development of a science-based adaptive process for determining and implementing management actions capable of generating improved outcomes. For example, an empirical indicator-based harvest strategy may represent a promising avenue for managerial action that has been successfully used to understand and manage other data-limited crab fisheries (Dowling et al., 2015). These strategies outline the data to collect, assessment approaches to undertake, and provide agreed-upon rules for adjusting harvest based on resulting indicator values. For example, stakeholders and managers collaborated to design and implement an empirical indicator framework to manage Queensland spanner crab (Dichmont & Brown, 2010). The framework originally set allowable harvest levels solely based upon fishery-dependent CPUE data, but as more information became available, the system was adapted to include fishery-independent indices and environmental cycles that influenced spanner crab abundance. After this adaptive system was implemented, catch rates grew to the highest on record despite initially high levels of uncertainty. There is no sign that spanner crab exploitation is unsustainable, showing that active and effective management is possible through adaptive co-management despite having no absolute measure of stock status. CA rock crab managers and stakeholders may consider a similarly adaptive strategy in order to better understand and manage their fishery. The exact decision rules used in such a strategy require careful deliberation and agreement among stakeholders, scientists, and managers and as such are outside the scope of this study. However, we do recommend considering spatial differences in rock crab stocks and fishery operations as well as species-level

differences in size and fecundity of CA rock crab when establishing monitoring, assessment, and management protocols (Hines, 1991, Culver et al., 2010).

Implementing an empirical harvest strategy clearly first requires identification and collection of indicators. Our recommendations include the collection of size, sex, CPUE, species composition, and discard rate data for CA rock crab because Culver et al. (2010) collected these data for this fishery in 2008, providing a reference for these values prior to the dramatic increase in rock crab landings after 2010. Costs of data collection may be kept to a minimum via collaborative fisheries research (CFR) programs, where fishers work with scientists or managers to collect needed information using their own fishing vessels and gear (Kay et al., 2012). Fishers typically require some level of fiscal compensation to offset the opportunity costs that arise from recording data instead of fishing, but partnerships with non-governmental organizations, academia, and/or the private sector can help fund such projects (Wilson et al., 2018). CFR also has the added benefit of enhancing stakeholder participation and buy-in for the management system, a vital component of assessing and managing any spatially structured or data-limited fishery (Orensanz & Jamieson, 1998, Smith et al., 1999, 2008, Aanesen et al., 2014, Dowling et al., 2015). CFR is particularly promising for CA rock crab due to fishers' willingness to participate in interviews and assist in interpreting results in this study, and because there is precedent for CFR in the SBC trap fisheries for rock crab (Culver et al., 2010) and spiny lobster (Kay et al., 2012). Our recommendations for CFR and indicator-based harvest strategies align with the needs of data-poor fisheries in CA and globally (Starr et al., 2010).

Our work shows that in the face of relatively little information, it is possible to glean insight on the impacts of fishing on target stocks from a suite of data limited assessment techniques. We acknowledge limitations of our approach, but effective managerial action does not require scientific certainty (Ludwig et al., 1993). Managers and stakeholders can take immediate steps to diagnose and respond to overfishing concerns, facilitating the design of appropriate harvest strategies ultimately capable of improving the management of data-limited fisheries.

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Figures

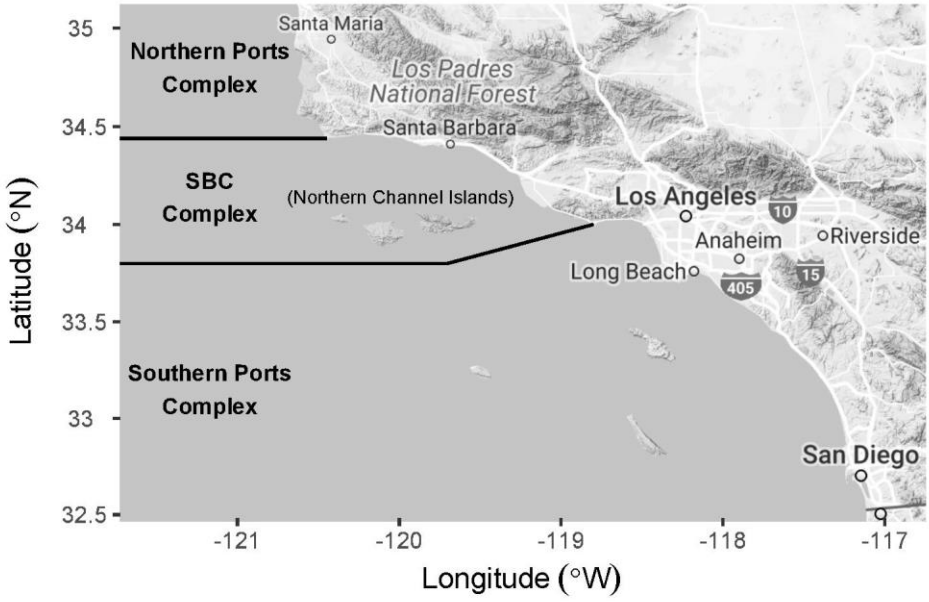

Figure 1. Map of study area along the Southern California coast. Black lines are the dividing lines between the three areas used in long-term spatiotemporal analyses: the Northern Ports Complex (top), the Santa Barbara Channel (SBC) Complex including the Northern Channel Islands (middle), and the Southern Ports Complex (bottom). Source: Kahle & Wickham (2017).

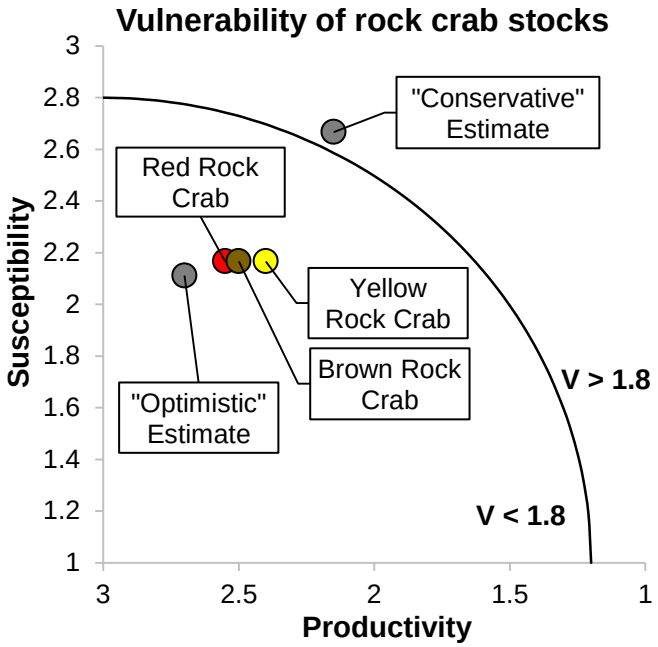

Figure 2. Vulnerability of rock crab stocks. PSA scores for each species of rock crab and sensitivity estimates described in main text. The black line represents the suggested cutoff between low and moderate vulnerability (V) from Patrick et al. (2009) and Cope et al. (2011).

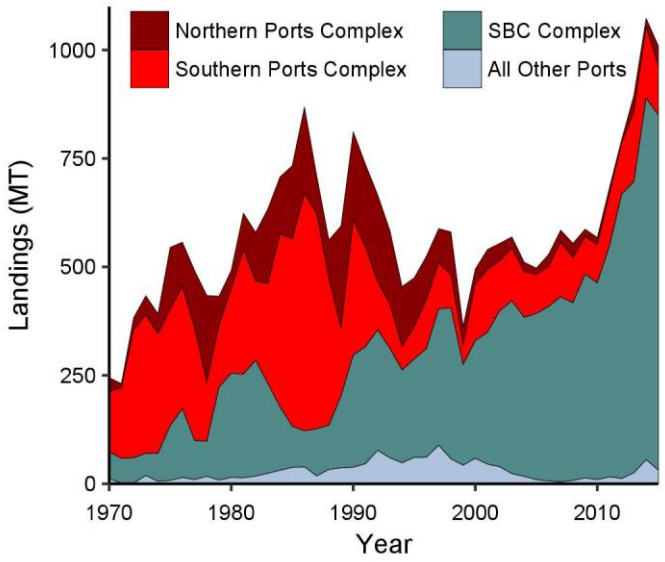

Figure 3. Statewide Landings of CA Rock Crab by Port Complex (1970-2015). Landings in metric tons (MT) are shown separately for the port complexes described in the text: the Northern Ports Complex (dark red), Southern Ports Complex (red), Santa Barbara Channel (SBC) Complex (blue-gray), and all other ports (light blue). Source: CDFW (2015).

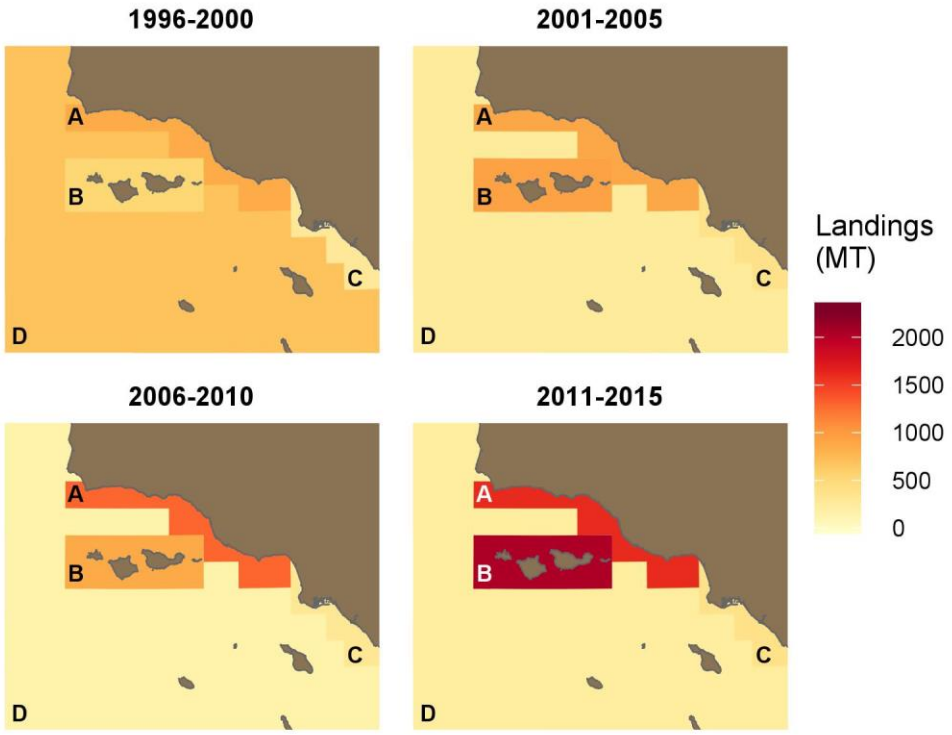

Figure 4. CA rock crab landings by region, 1996-2015. Landings in metric tons (MT) are shown in four 5-year increments from 1996-2015 for four regions: (A) the Santa Barbara Channel (SBC) mainland coast, (B) the Northern Channel Islands, (C) the southern mainland coast, and (D) all other blocks. Source: CDFW (2015).

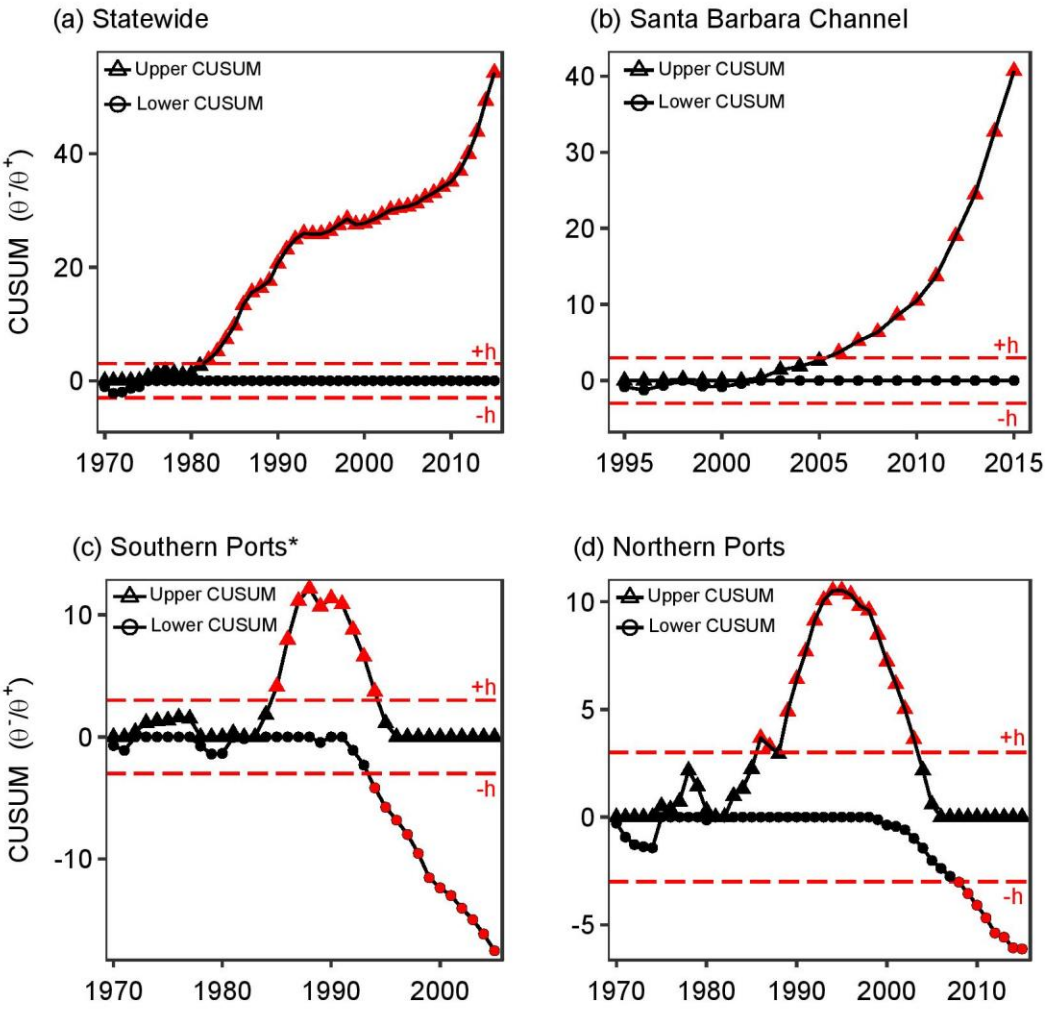

Figure 5. CUSUM control charts of CA rock crab landings by region (1970-2015). Upper (θ^+) and lower (θ^-) CUSUM results for (a) the entire statewide CA rock crab fishery, (b) the Santa Barbara Channel (SBC Complex), (c) the Southern Ports Complex, and (d) the Northern Ports Complex. Dashed red lines show the upper and lower decision interval bounds ($\bar{X} \pm h$). Black points indicate "in-control" signals and red points indicate "out-of-control" signals (see section 2.3.3 for explanation). Source: CDFW (2015). *The control chart for the Southern Ports stops in 2005 for aesthetic purposes, but θ^- values continued to decrease through 2015.

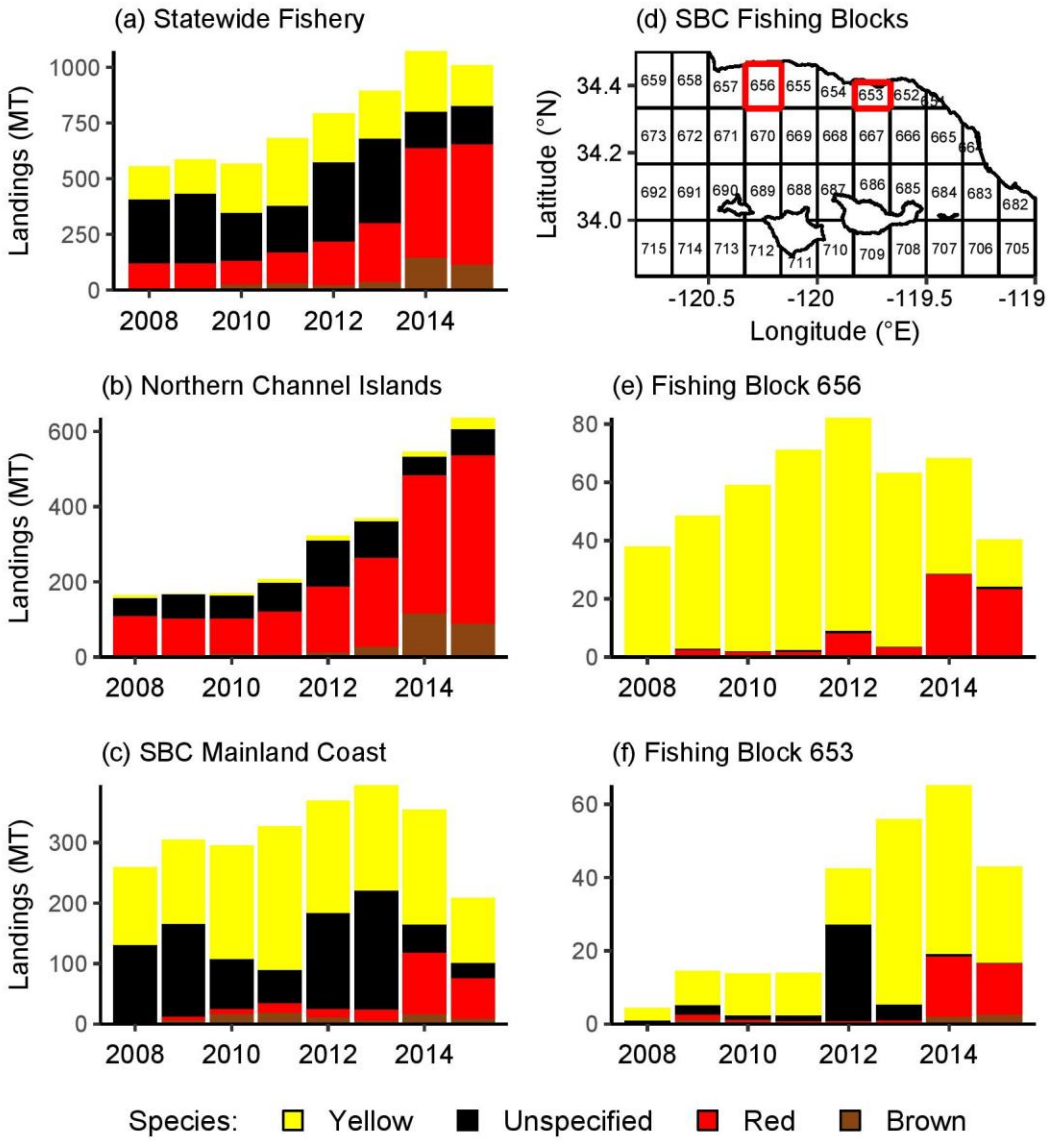

Figure 6. CA rock crab landings by species and region (2008-2015). Species composition of landings in metric tons (MT) for (a) the entire statewide fishery, (b) the Northern Channel Islands, and (c) the Santa Barbara Channel (SBC) mainland coast. A map of fishing block locations in the SBC shows the two blocks with reliable data reporting discussed in section 3.1.4 (d; red rectangles), and their species composition is shown (e-f). Source: Parker (2003), CDFW (2015).

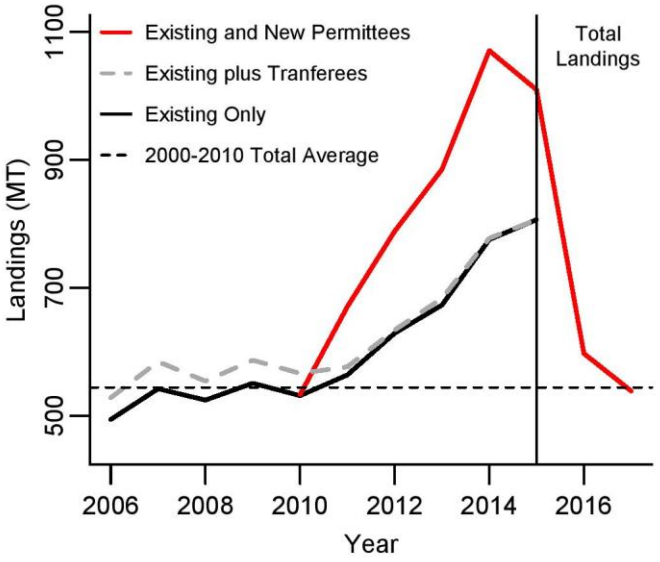

Figure 7. Statewide landings of CA Rock Crab by permit type, 2006-2017. Landings in metric tons (MT) from 2006-2015 made by: existing and new permittees combined (red solid line), existing permittees and transferees combined (gray dashed), existing permittees only (black solid), and average landings from 2000-2010 as a baseline reference (black dashed). "New permittees" refers to fishers who bought their permits after 2010, "transferees" refers to the fishers who sold those permits from 2011-2015, and "existing permittees" refers to fishers who held permits since 2006 or before and were uninvolved in the transfer process. Permit information is not yet available for 2016-2017, but total landings are shown (red solid). Source: CDFW (2015, 2017).

Appendix A

Table S1. Summary of information input into FishPath software. CA rock crab fishery information across the five categories in FishPath. Sources are indicated unless the information was gathered via personal communication and expert judgment.

Data Category	Variable	S. CA rock crab estimate	Description
Biological/life history attributes of relevant species*	**Minimum size at maturity (S_m)**	43-89 mm	Red[1] and brown[2] rock crab have a smaller estimated S_m than yellow crab[3,4]
	Maximum size	145 to > 200 mm	Brown rock crabs are the smallest[2,3,5], red rock crabs are largest[3,5]
			Males reach larger sizes than females
	Longevity	4-7 years[2,6]	Estimates based on projections of the number of instars and borrowing from other species.
	Age at maturity (A_m)	1-2 years	1 yr for red[1], 1.5-2 yr for brown[2], 2 yr for yellow[6,7].
	Habitat	Variable	Primarily rocky reefs (red), soft sediment (yellow), or both (brown)
Available Data	**Commercial landings**	Landings Receipts since 1950[8]	Not spatially specific until 1996 (> 90% accurately reported by fishing block)
			Species unspecified until 2007. > 50% specified by 2010, > 70% by 2014
		Effort	Number of landings receipts can be a proxy
	Other data	Fishery Dependent	CPUE, size frequency, and sex composition data was recorded in 2008[9]. There is no logbook to record CPUE or effort data.
		Fishery Independent	Footnotes provide some information on size distribution, larval survival/growth, and so forth
Fishery operational characteristics	**Trip length**	Variable	Range from 1-day to 4-day overnight trips
	Gear	Entirely trap-based	Traps can be set individually, two on one buoy, or many placed side-by-side
			Traps have 3.25 inch (82.5 mm) escape rings
	Fishing practices	Discards	Berried females thrown back by many fishers
		Bycatch	Lingcod, octopus, kellet's whelk, sheep crab
Socio-economic indicators/ characteristics	**Market**	Domestic	Some fishers sell at local markets themselves
			Some sell to a buyer for local restaurants
		Expanded	Some may sell to developing markets outside CA (personal communication)
	Livelihoods	Reliance	> 100 fishers, often the primary income source
Governance context	**Size limit**	108 mm (4.25 inch)	Applies to all species, genders and locations
	Permit system	124 permits	Transfers allowed at a rate of 5 per year. There are a 163 permits in CA, 124 of which are restricted access southern permits.
	Other Limits	None	There are no catch, effort or season restrictions

[1]Orensanz & Gallucci 1988, [2]Carroll 1982, [3]Carroll & Winn 1989, [4]Shields et al. 1991, [5]Parker 2003, [6]Shields 1991, [7]Anderson & Ford 1976, [8]CDFW 2015, [9]Culver et al. 2010; [*]Most of the sources used to compile this information are not site-specific to the SBC

II. Collaborative research reveals cryptic declines within the multispecies California rock crab fishery

Abstract

The southern California rock crab fishery targets stocks comprised of three species: red (*Cancer productus*), yellow (*Metacarcinus anthonyi*), and brown rock crab (*Romaleon antennarium*). Fishers have expressed concern about the sustainability of the fishery due to increased fishing effort over the past decade, and because it is managed as one assemblage despite distinct life history differences among the species. We collaborated with fishers to test for stock-specific declines in key fishery-dependent indicators by replicating a 2008 study in 2016-2017 and comparing indicator values between years using multiple regression techniques. Indicators included spatially explicit species-level data for size, catch-per-unit-effort (CPUE), discard rate, sex composition, and trap location and depth across the heavily fished Santa Barbara Channel and Northern Channel Islands. Results showed significant declines in male size, overall CPUE, and proportion of crab landed versus discarded for heavily targeted stocks, translating to fewer pounds per trap and potential financial losses for fishers. Fishing and environmental conditions may have both contributed to stock declines. Evidence of decline differed substantially across space, species, and sex. We suggest that a spatially explicit and adaptive approach to empirically managing southern California rock crab may help to protect fishers from financial loss and avoid continued depletion of certain stocks, and we show that relatively simple collaborative approaches can provide defensible insight into complex systems.

1. Introduction

Marine fisheries that target multispecies assemblages are highly susceptible to overfishing when fishing remains profitable overall, even as some stocks collapse (Burgess et al., 2013). This is especially true in data-limited circumstances where the assemblage is managed as one stock due to a lack of species-specific demographic information, including growth rate, size at maturity, and fecundity (Pauly, 1979; Hilborn and Walters, 1992; Botsford et al., 1997; Hilborn et al., 2004). A paucity of information regarding the spatial structure of many target populations compounds the problem and further challenges management, an issue that has arisen frequently for demersal species (Hutchinson, 2008; Gunderson et al., 2008). A "tyranny of scale" emerges in cases where management is executed at a spatial scale larger than the scale at which a population, or sub-population, functions demographically and is connected through larval dispersal (Prince et al., 1998; Prince, 2005). Widespread larval dispersal may not compensate for localized overfishing of demersal organisms, such as groundfish and crabs, whose populations experience high levels of self-recruitment and often consist of genetically distinct subpopulations (Smedbol and Wroblewski, 2002; Swearer et al., 2002; Gunderson and Vetter, 2006; Corgos et al., 2011; Grant et al., 2011). Incorporating spatial information into management of sedentary species is therefore critical for improving the sustainability of localized stocks and ecosystems (Pikitch et al., 2004; Gunderson et al., 2008; Gutiérrez et al., 2011).

Including spatial information in stock-specific biomass-based assessment and management strategies is highly desirable and beneficial, but it can be challenging. Some highly profitable and sustainable crab fisheries, such as the Bering Sea and Aleutian Islands (BSAI) king and tanner crab fisheries, provide examples where such robust management

has been possible and advantageous. However, data-rich, spatially explicit management as executed in the BSAI crab fisheries is usually prohibitively expensive (Prince, 2003; Guan et al. 2013). It is also inherently challenging to manage sedentary species that are difficult to age, have highly uncertain stock-recruitment relationships, and display high spatial variability in growth, mortality rates, and other key metrics used to estimate biomass and maximum sustainable yield (Zheng, 2005; Szuwalski and Punt, 2012; Punt et al., 2013; Szuwalski et al., 2015). Even distinct subpopulations of various crab species exhibit spatially variable life histories (Bennett, 1995; Botsford et al., 1998; Weber and Levy, 2000; Gerhart and Bert, 2008). As a result, crab fisheries worldwide generally lack sufficient data or resources for effective spatial management according to quantitative and/or model-based assessments (Costello et al., 2012; Worm and Branch, 2012; Carruthers et al., 2014; FAO, 2016). Many crab fisheries thus remain unmanaged. For those that are managed, input-based controls such as size-, sex-, and/or season-based regulations are often implemented despite leading to overcapacity and serial depletion in many well-documented cases (Orensanz et al., 1998; Fina, 2005; Salomon et al., 2007). When possible, spatially explicit approaches to assessment and management are preferable to uniformly applied input controls or allowable catch limits for sedentary stocks, especially when treating multiple stocks or species as one assemblage (Jamieson and Campbell, 1998; Hutchinson, 2008; Ying et al., 2011). Directly or indirectly accounting for spatial structure has proven essential for ensuring the long-term success of fisheries targeting sedentary invertebrates (Orensanz and Jamieson, 1998), so the challenge is to develop approaches to stock monitoring and assessment that promote efficient, effective spatial-based management.

Empirical indicator-based frameworks are a promising alternative to conventional model-based assessment and management techniques that rely on estimating standing biomass, fishing mortality rates, and sustainable yields (Harford et al. 2019). Empirical indicators are measured directly from data – not derived through modeling – and can include total catch, size, species composition, and catch-per-unit-effort (CPUE; Dowling et al., 2015a). Adaptive harvest strategies are constructed around these indicators as a cost-effective means for sustainably managing data-limited fisheries (Dowling et al., 2015b; Bentley, 2015). The first step towards building such a strategy is coordinating the collection of reliable and spatially specific indicator data, which is usually too costly for a governing body to obtain. Involving stakeholders in collaborative fisheries research (CFR) provides scientifically valid, localized information at substantially lower costs relative to governmental or private research practices (Johnson and van Densen, 2007). In many cases, CFR also increases transparency of the management process, improves communication among researchers, managers and stakeholders, incorporates fishers' expert knowledge into assessment and management, and increases stakeholder support for science-based management (Johnson, 2010; Yochum et al., 2011). CFR has a long history of use in fisheries management, and recently it has received much attention as a valuable tool for improving monitoring, assessment, and/or management of sedentary marine resources (Hartley and Robinson, 2008; Wiber et al., 2009; Kay et al., 2012; Wilson et al., 2012; Ebel et al., 2018). Here, we examine and compare empirical indicators collected through a collaborative at-sea sampling program (CASP; see Culver et al., 2010; Yaeger et al., 2017) conducted in 2008 and 2016-2017 to determine whether declines have occurred for spatially heterogeneous stocks of southern California (CA) rock crab. Our specific

objective was to work with fishing partners and managers to test for stock-specific declines in indicator values using a low cost, repeatable program that could be used over the long term to enhance management. Our case study demonstrates a need to assess and manage sedentary species as individual stocks, supports the utility of low cost CASPs for collecting the information needed to manage at a stock-specific level, and shows that relatively simple approaches can give valuable insight into complex social-ecological systems.

2. Methods

2.1 Collaborative Research for the Southern CA Rock Crab fishery

We recognized a need to assess the status of the southern CA rock crab fishery upon hearing concerns from the fishing community. Trap fishing effort and landings increased tremendously for red, yellow, and brown rock crabs from 2010-2015 due to increased market demand and legalization of five permit transferals (sales) per year in this limited entry fishery (Fig 1; Fitzgerald et al., 2018). The increase was particularly dramatic at the highly productive Northern Channel Islands (CDFW, 2017). Trapping studies indicate that rock crab are susceptible to localized depletion (Carroll and Winn, 1989; Parker, 2003), partially due to their sedentary life history and relatively restricted movement (Carroll, 1982; Boulding and Hay, 1984; Winn, 1985; Carroll and Winn, 1989). Overfishing was suspected for some stocks in part because a single size limit applies to all three CA rock crabs despite interspecific biological differences, sexual dimorphism, uncertain size at maturity estimates, and apparent spatial variation in intraspecific life history. However, biological data limitations for CA rock crab prevent reliable assessment of stock status. Given that the only data for the fishery is total landings data, we identified an opportunity

to build upon a 2008 CASP for rock crab (Culver et al. 2010) in a way that facilitates assessment of the fishery despite data limitations.

At our request and with our assistance, seven commercial fishers followed the protocols developed in 2008 to collect spatially specific size, sex, CPUE, and discard rate data during select fishing trips for each rock crab species in 2016-17, using the same fishing vessels and locations as in 2008. Our goal was to quantify stock-level declines in 2016-17 relative to 2008. We define a stock as a particular species in a particular location (mainland CA coast or Channel Islands), and further separate stocks by sex when possible. As stock status cannot be determined for rock crab, we define stock decline or depletion as significant changes in indicator values that reflect worse fishery outcomes in 2016-17 relative to 2008 – not the classical definition of depletion related to stock reduction below maximum productive capacity (Van Oosten, 1949). A decline in sex composition refers to a decreased presence of males in the catch because male rock crabs are preferentially targeted as a result of market demand, and size and abundance typically declines faster for male than female crabs in fisheries targeting sexually dimorphic species (e.g., Abbe, 2002, Smith and Jamieson, 1991). A decline in terms of discard rate refers to a higher proportion of crabs discarded, meaning that fishers were unable to catch as many marketable crabs due to small sizes and/or poor quality. We monitored and assessed the reasons why crabs were discarded because discard rate can change for many reasons unrelated to fishing, and we also examined the influence of trap depth on species composition in both periods.

Stakeholders helped to interpret our results, which showed significant declines for heavily targeted stocks between 2008 and 2016-17, translating to fewer pounds per trap and potential financial losses for fishers. We examined how indicators varied by species,

sex, and location to help managers and fishers (i.e., "stakeholders") understand and address variation within the fishery. Levels of decline varied between stocks because stocks responded differently to heavy fishing pressure under the uniformly applied management approach.

2.2 General approach

The objective of this study was to replicate an intensive CASP to compare key indicators of rock crab fishery status in 2016-17 versus 2008. These two studies bookend the sharp increase in rock crab fishing effort and landings from 2010-2015 and a subsequent decline in landings back to pre-2010 levels (Fig. 1). We considered various information streams to evaluate whether intensified fishing or environmental conditions drove indicator changes, but our intent was not to provide definitive proof of overfishing – assigning causality to detected changes is not possible with our research design. Rather, our analyses aim to test whether changes in size, CPUE, discard rate, and sex composition indicate stock declines that negatively impacted fishers. We used multiple regression techniques that controlled for individual fishing vessels (F/Vs) to compare indicator values between study periods. We considered size and CPUE to be our most direct, reliable indicators of stock decline, and we present comparative regression results only for landed crab (kept and sold, not discarded), because that is what directly determines revenue. By focusing on landed crabs, we directly quantified those changes affecting fishers. Every fisher retained and sold their commercial catch in this study, so they were directly motivated to obtain catch with the highest value (i.e., large crabs, high number of crabs landed per trap). By contrast, fishers were not directly motivated to maintain low discard rates or a particular sex composition, so we used these two indicators to complement size

and CPUE findings rather than using them to indicate depletion independently. By controlling for F/V and discard status and considering supplemental information in our analyses, we attempt to generate valuable insight into a complex multispecies and spatially structured fishery that can be used to improve long-term management of the resource.

2.3 Study Site

The southern CA rock crab fishery targets male and female red (*Cancer productus*), yellow (*Metacarcinus anthonyi*), and brown (*Romaleon antennarium*) rock crab. Fishers are required to land whole crabs, although claw-only markets also exist. The fishery primarily operates across the several thousand square kilometers of the SBC. Circulation patterns of the SBC produce pronounced spatial variation in nutrient availability, characterized by relatively high primary and secondary production in the western and offshore portions of the ecosystems, and relatively low productivity in eastern and inshore areas (Harms and Winant, 1998; Hamilton et al., 2011; Wilson et al., 2012). Many organisms consequently reach larger sizes at the Northern Channel Islands than elsewhere in the SBC (Wilson et al., 2012). Yellow rock crab are found mainly along the mainland coast where their preferred habitat of sand and soft bottom occurs, while red and brown rock crab are found throughout the SBC in rocky reef areas (Carroll and Winn, 1989; Parker, 2003; CDFW, 2017). Life history data are sparse for SBC rock crabs, but the three species exhibit biological and ecological differences that have important management implications. For example, all three species are sexually dimorphic, reach different maximum sizes, live in different habitats, exhibit varying relative abundances along the west coast of North America, and vary in reproductive potential (Carroll & Winn 1989;

Hines, 1991). Table S1 in Fitzgerald et al. (2018) provides a comprehensive summary of available life history information for CA rock crab.

Spatial fishing patterns reflect the physical distance between the mainland coast and the islands. Fishers rarely target both locations in the same fishing trip and do not often move gear between the two areas, and catch composition differs markedly in each region (CDFW, 2015). All three species had become highly marketable by 2016, although coastal brown rock crab were actively avoided in 2008 due to low market demand. Management restricts the number of available permits and regulates catch through a minimum size limit of 4.25-inch (108 mm) carapace width (CW) for males and females of all three species, but there are no other limits on catch or effort.

2.4 Sampling methods and fishing partners

Our sampling methods were virtually identical to those of Culver et al. (2010). Fishers recorded the number of each crab species that were landed and discarded at sea for every trap on every fishing trip. For every fifth trap pulled, fishers also recorded GPS coordinates, the depth of the trap, the sex of each crab, the size of each crab (CW, mm), whether females were egg-bearing, and the reason discarded as applicable (soft, small, missing claw(s), shell imperfections, gravid, or other). The only sampling difference in this study was recording size from the gap between the two most posterior lateral spines, whereas 2008 size data was recorded from the widest spines (the gap measurement is more reliable because spines can be broken or abraded). We converted crab sizes in 2008 to gap-based size data using species- and sex-specific observations of both widest spine and gap measurements (n = 583; S. Fitzgerald, unpubl. data). Datasheet templates and the complete sampling methodology provided to fishers are in Appendix A and B. Fishers from seven different

fishing vessels (F/Vs) took 29 trips from April 2016 to December 2017, with the majority of trips taken to similar locations fished in the earlier study (Culver et al. 2010). Two of the fishers were participants in the 2008 study, and three of the fishers owned and operated a F/V used in the 2008 study. Each of the three new participants was trained in commercial fishing practices by the previous F/V owners who participated in 2008. We also had two fishers in our study who owned and operated vessels that were not part of the 2008 study. Their information was excluded from comparative analyses because analyses controlled for differences among F/Vs in order to accurately assess fishery-related changes. For size, sex, and discard rate analyses each crab was considered an independent sample; for CPUE each trap pull was considered an independent sample. Table 1 provides overall sample sizes for both studies, with and without the new F/Vs.

2.5 Data analysis

We used multiple linear regression to assess changes in size, CPUE, discard rate, and sex composition between the two studies for every combination of species and location (SBC coast versus islands). We controlled for sex in our size regressions and controlled for discard status (i.e., whether a crab was landed or discarded) in regressions for size, CPUE, and sex composition. We did not control for season or individual year in our presented analyses because results remained similar when controlling for season or restricting analyses to 2016 or 2017 data only. We performed each regression separately for the coast and islands due to the differenced outlined above. We included fishing vessel (F/V) as a fixed effect to control for differences in fishing practices among vessels including trap configuration, target markets, and the spatial distribution of traps. Accounting for F/V also allowed us to control for location at a finer scale than coast versus islands because each

F/V exploited similar locations in both studies. There were also disproportionate sample sizes between time periods and locations due to varying effort by one or more fishermen, so controlling for F/V avoided bias stemming from unequal sample sizes from individual fishers. We used data from only the five F/Vs that participated in both studies to avoid bias introduced by new fishing practices or locations. All regression analyses were performed in R (R core team, 2016) using heteroscedasticity-robust Huber-White standard errors[1] (MacKinnon and White, 1985). We also used data from two or more fishers in every analysis to protect fishers' anonymity. Details of each regression model are below.

2.5.1 Size

First, we investigated whether crab sizes changed between 2008 and 2016-17 for every combination of species, sex, year, and discard status (landed or discarded at sea). We used multiple linear regression to assess size changes, coding each combination as its own dummy variable (value = 0 or 1) and F/V as a factor. For the islands we used the equation

$$Size(mm) = \beta_0 + \beta_1 * FV1 + \beta_2 * RM08K + \beta_3 * RM16K + \beta_4 * RF08K + \beta_5 * RF16K + \beta_6 * BM08K + \beta_7 * BM16K + \beta_8 * BF08K + \beta_9 * BF16K + \beta_{10} * RM08D + \beta_{11} * RM16D + \beta_{12} * RF08D + \beta_{13} * RF16D + \beta_{14} * BM08D + \beta_{15} * BM16D + \beta_{16} * BF08D + \beta_{17} * BF16D + \varepsilon, \quad \text{(Eq. 1)}$$

where β_0 is the intercept, every other β value refers to each dummy variable coefficient, *FV1* refers to the non-reference F/V, *R* and *B* respectively refer to red and brown rock crab, *M* and *F* respectively refer to male and female crab, *08* and *16* respectively refer to 2008 and 2016-17, *K* and *D* respectively refer to kept (landed) and discarded crab, and ε is an error term. The F/V reference level was selected randomly in every analysis to avoid revealing individual fishers' data. The equation for the coast was

[1] The significance of model results was largely unchanged when changing standard error specifications, including using non-robust standard errors, alternative robust standard error estimators, or clustering standard errors on individual traps

$$Size(mm) = \beta_0 + \beta_1 * FV1 + \beta_2 * FV2 + \beta_3 * RM08K + \beta_4 * RM16K + \beta_5 * RF08K + \beta_6 * RF16K + \beta_7 * BM08K + \beta_8 * BM16K + \beta_9 * BF08K + \beta_{10} * BF16K + \beta_{11} * YM08K + \beta_{12} * YM16K + \beta_{13} * YF08K + \beta_{14} * YF16K + \beta_{15} * RM08D + \beta_{16} * RM16D + \beta_{17} * RF08D + \beta_{18} * RF08D + \beta_{19} * BM08D + \beta_{20} * BM16D + \beta_{21} * BF08D + \beta_{22} * BF16D + \beta_{23} * YM08D + \beta_{24} * YM16D + \beta_{25} * YF08D + \beta_{26} * YF16D + \varepsilon, \quad \text{(Eq. 2)}$$

where *Y* refers to yellow rock crab and *FV2* refers to a second non-reference F/V, with all other variables similar to those in Eq. 1.

After performing the regressions, we tested individual dummy variable coefficients from 2008 versus 2016-17 against one another using the 'linearHypothesis()' function in the R package 'car' (Fox and Weisberg, 2011; Fox et al., 2013) to test whether crab size differed between years for each species, sex, and discard combination. The function calculates an *F* statistic by comparing the original model with a restricted model. For example, testing the original model in Eq. 1 versus the same model with the applied restriction $\beta_3 = \beta_2$ identifies whether the size of landed male red rock crab at the Channel Islands significantly differed between 2008 and 2016-17 (i.e., RMI08K = RMI16K). The difference in coefficient values (e.g., $\beta_3 - \beta_2$) also reflects the mean size difference (in mm) between years after controlling for F/V and the other model factors. Additionally, we asked whether size changes of males and females were of a similar magnitude for each species (e.g., $\beta_3 - \beta_2 = \beta_5 - \beta_4$ from Eq. 1). We present coefficient test results only; complete model results are in the supplementary material. Finally, we generated histogram + density plots using data from all seven F/Vs to visualize variation in crab size frequency by species, sex, location, and year.

2.5.2 CPUE

Second, we investigated whether CPUE (number of crabs per trap, calculated from the total number of crabs caught divided by the total number of traps fished) changed between

2008 and 2016-17 for every combination of species, location, and discard status. Using multiple linear regression, we assessed CPUE changes at the islands:

$$CPUE_i = \beta_{0i} + \beta_{1i} * Year + \beta_{2i} * FV1 + \varepsilon_i, \quad \text{(Eq. 3)}$$

and along the coast:

$$CPUE_i = \beta_{0i} + \beta_{1i} * Year + \beta_{2i} * FV1 + \beta_{3i} * FV2 + \varepsilon_i. \quad \text{(Eq. 4)}$$

We assessed CPUE separately for every combination of species and discard status, so in both equations the subscript *i* denotes a specific combination of species (red or brown, as well as yellow along the coast) and discard status (landed or discarded), resulting in four regressions at the islands and six regressions along the coast. *Year* was coded as a factor (reference = 2008). We did not consider sex, because it was recorded only for every fifth trap, and we used the entire dataset in CPUE analyses. Here, the main coefficient of interest is the value of β_1 for each stock, which indicates how CPUE changed in 2016-17 relative to 2008 after controlling for F/V. A negative β_1 value means CPUE decreased relative to 2008 and a positive β_1 value means CPUE increased. Finally, CPUE of all three species combined may be the most important indicator for fishers because species-specific CPUE can be influenced by market demand, but by 2016 all species had become highly marketable. As such, we modeled overall CPUE as a function of year and F/V for the islands:

$$CPUE_{AllKeptCrab} + CPUE_{AllDiscardedCrab} = \beta_0 + \beta_1 * Year + \beta_2 * FV1 + \varepsilon, \quad \text{(Eq. 5)}$$

and for the coast:

$$CPUE_{AllKeptCrab} + CPUE_{AllDiscardedCrab} = \beta_0 + \beta_1 * Year + \beta_2 * FV1 + \beta_2 * FV2 + \varepsilon. \quad \text{(Eq. 6)}$$

2.5.3 Discard rate and reason for discard

2.5.3.1 Discard rate

Third, we assessed changes in the discard rate of captured crabs between 2008 and 2016-17 for every combination of species and location to test whether fishers retained more crabs in 2016-17. We performed binomial logistic regression to calculate the probability of discarding a crab at the islands:

$$Discard(0 = no, 1 = yes) = \beta_1 * FV1 + \beta_2 * R08 + \beta_3 * R16 + \beta_4 * B08 + \beta_5 * B16 + \varepsilon, \quad \text{(Eq. 7)}$$

and along the coast:

$$Discard(0 = no, 1 = yes) = \beta_1 * FV1 + \beta_2 * FV2 + \beta_3 * YC08 + \beta_4 * YC16 + \beta_5 * RC08 + \beta_6 * RC16 + \beta_7 * BC08 + \beta_8 * BC16 + \varepsilon. \quad \text{(Eq. 8)}$$

In both models, we coded a discarded crab as a 1 (landed crab = 0) and generated dummy variables for each combination of species and year. As with CPUE, discard rate analyses were not sex-specific because we used data from every trap. Results were transformed from log odds to marginal probabilities, and coefficient tests (e.g., $\beta_3 = \beta_2$ from Eq. 7) then determined whether discard probability changed significantly between periods for each species at each location. The difference in coefficient values represents the mean difference in probability of discarding a given species of crab at each location after controlling for F/V. We suppressed model intercepts because results were more concise and easier to interpret than models that included intercepts (not shown), but including intercepts did not change coefficient test results.

2.5.3.2 Discard reason

We used chi-squared testing for equal proportions to determine whether the reasons for discarding crabs changed between periods for each species and location. Results informed our interpretation of changes in discard rate and CPUE. If fishers were discarding more

crabs because the crabs were "soft" (recently molted), gravid, or of poor quality, we would not attribute those changes to stock depletion. Conversely, if fishers were discarding more crabs only because they were smaller than legal size, stock depletion is a likely explanation. *Post hoc* examination of standardized residuals determined which changes were the most significant.

2.5.4 Sex Composition

Fourth, we investigated whether the sex composition of captured crabs differed between periods for every combination of species, location, and discard status. We used binomial logistic regression to model the probability of capturing a male crab (female = reference category) at the islands:

$$Sex\ (0 = F, 1 = M)\ = \beta_1 * FV1 + \beta_2 * R08K + \beta_3 * R16K + \beta_4 * B08K + \beta_5 * B16K + \beta_6 * R08T + \beta_7 * R16T + \beta_8 * B08T + \beta_9 * B16T + \varepsilon, \quad \text{(Eq. 9)}$$

and along the coast:

$$Sex(0 = F, 1 = M)\ = \beta_1 * FV1 + \beta_2 * FV2 + \beta_3 * R08K + \beta_4 * R16K + \beta_5 * B08K + \beta_6 * B16K + \beta_7 * Y08K + \beta_8 * Y16K + \beta_9 * R08T + \beta_{10} * R16T + \beta_{11} * B08T + \beta_{12} * B16T + \beta_{13} * Y08T + \beta_{14} * Y16T + \varepsilon. \quad \text{(Eq. 10)}$$

We generated dummy variables for every combination of species, year and discard status, transformed results from log odds to marginal probabilities, and used coefficient tests (e.g. $\beta_3 = \beta_2$ from Eq. 9) to determine whether the probability a crab was male changed between periods. We suppressed model intercepts as in section 2.4.3.1. Including intercepts did not change coefficient test results.

2.5.5 Summarized indicator values versus regression results

To assess the value of controlling for F/V and discard status, we first calculated simple means and standard errors for the main dependent variables (male size, female size, CPUE, discard rate, and sex composition) without controlling for F/V. We then compared those

values to regression model outputs for landed crabs from every location to determine whether simple summary statistics accurately reflected stock-level indicator changes in the rock crab fishery. Summary statistics that include discarded crabs are in the supplementary material.

2.5.6 Depth analyses

Finally, we investigated how trap depth influenced species composition of the catch and whether trap depth changed between periods to facilitate interpretation of regression results. We did not include depth in the regressions described above because it was recorded only on every fifth trap. Also, fishers can change the depth at which they fish at will, making trap depth irrelevant to this study as we were not evaluating whether fishing is better at one depth or another. For our evaluations, indicator changes reflect general outcomes for fishers regardless of depth. However, depth analyses can provide insight explaining indicator patterns. If species composition changes with depth, species-specific CPUE changes may reflect a change in trap depth rather than a change in abundance. We used multinomial logistic regression to assess how trap depth influenced the probability of catching a given species using the equation

$$Speciescaught = \beta_0 + \beta_1 * Depthoftrap(ft) + \varepsilon, \quad \text{(Eq. 11)}$$

where *Species caught* was a factor with brown rock crab as the reference level. We performed regressions separately for the coast and islands and included all years of data from every fifth trap from the F/Vs involved in both studies. For simplicity, the reported analyses do not account for F/V, year, or sex because model outcomes were similar when controlling for any or all of these independent variables. We report results in odds ratio (OR), where values greater than one show that the odds of capturing a given species (red

or yellow) increased with depth relative to the odds of capturing the reference species (brown).

We also modeled depth as a function of year and F/V at each location to determine whether fishers' trap depth changed between periods using the equation:

$$Depthoftrap(ft) = \beta_0 + \beta_1 * Year + \beta_2 * F/V + \varepsilon. \quad \text{(Eq. 12)}$$

F/V and *Year* were both coded as factors (2008 = reference year), and a positive β_1 value means traps were set deeper in 2016-17 relative to 2008.

2.5.7 Weight per trap calculations and revenue estimates

To examine the potential financial impact of the indicator changes we identified in this study, we calculated the difference in overall weight per trap for fishers between studies, then used this difference to estimate changes in revenue per trap. We used our model coefficients for size, CPUE, and sex composition as well as *in situ* length-weight observations (S. Fitzgerald, unpublished data) to calculate the average difference in weight of crab landed per trap between studies. We then converted crab weights to $USD using the 2016 average price per pound (CDFW, 2017).

3. Results

We did not include yellow rock crab at the islands in any analyses and do not present results from size or sex analyses for brown rock crab along the coast. Yellow rock crab are not targeted at the islands and coastal brown rock crabs were not targeted in 2008, so they represent incidental catch with low sample sizes ($n < 30$). All other regression results for landed crabs are presented below (see supplementary material for results including discarded crab).

3.1 Size

Size of male brown and red rock crab from the islands decreased by 4.23 mm ($p < 0.05$) and 8.12 mm ($p < 0.001$), respectively, between the two study periods (Table 2; Table S1-S3). Sizes also decreased 7.28 mm more for male than female red rock crab at the islands ($p < 0.001$; Table S3). Along the mainland SBC coast, mean size of male yellow crab decreased by 3.80 mm ($p < 0.001$) but did not change for females (Table 3; Table S1; Table S4-S5). Size did not significantly increase for any species, location, sex, or discard status ($p > 0.05$; Table 2-3; Table S2-S5).

Sizes were highly variable among species, locations and sexes. In general, rock crabs were larger at the islands than along the coast and males were larger than females (Fig. 2). Males obtained sizes 20-40 mm larger than females for every species and location (Fig. 2). Red rock crab were the largest species, followed by yellow then brown rock crab.

3.2 CPUE

CPUE decreased significantly for most species and locations (Table 4, 5). At the islands, CPUE decreased by 0.64 crabs per trap for brown rock crab ($p < 0.001$) and by 0.94 crabs per trap overall ($p < 0.05$; Table 4). There was no significant decrease for red rock crab (CPUE decreased by 0.30 crabs per trap; $p = 0.46$; Table 4). Along the mainland coast, CPUE decreased for yellow and red rock crab by 2.72 and 2.08 crabs per trap, respectively ($p < 0.001$), whereas CPUE increased for brown rock crab by 0.57 crabs per trap ($p < 0.001$; Table 5). Overall CPUE decreased by 4.23 crabs per trap along the coast ($p < 0.001$). Overall CPUE of discarded crab increased by 2.05 crabs per trap along the coast ($p < 0.001$) and did not change at the islands ($p = 0.36$; Table S6-S7).

3.3 Discard rate and reason for discard

3.3.1 Discard rate

Regression results showed that discard probability in 2016-17 was 2.7% higher than in 2008 for red rock crab at the islands, 10.2% higher for coastal yellow rock crab, and 5.7% lower for brown rock crab at the islands ($p < 0.01$ in all cases; Table 6, Table S8). While significant, estimates indicating a 24.2% increase in discards of coastal brown rock crab ($p = 0.001$; Table 5) should be treated with caution because this stock was not targeted in 2008.

3.3.2 Discard reason

The reasons fishers discarded crabs significantly changed only for red rock crab at the islands (χ^2 (6) = 89.928, $p < 0.001$) and yellow rock crab along the coast (χ^2 (6) = 195.38, $p < 0.001$). Examination of standardized residuals showed that the most substantial changes for red rock crab at the islands were 33.3% fewer discards due to imperfections and 31.5% more discards due to missing claws, followed by 3.0% more discards due to the presence of eggs (Fig S1). The most substantial change for coastal yellow rock crab was 36.1% fewer discards due to softness, followed by 12.1% more discards due to small size and 7.7% more discards due to the presence of eggs (Fig S2).

3.4 Sex composition

Regression analysis to test the influence of species, discard status, and year on sex composition showed that the probability of landing a male crab decreased by 9.3% for red rock crab at the islands and 4.8% for yellow rock crab along the coast ($p < 0.05$; Table 7). Changes were insignificant for all other combinations except for discarded red rock crab along the coast, which were 26.5% more likely to be male in 2016-17 (Table S9-S10).

3.5 Comparison of summarized indicator values to regression results

Table 8 summarizes regression results from sections 3.1–3.4 (Table S11 includes discarded crabs). Summarized statistics for landed crabs (simple means and standard errors; Table 9) generally agreed with results from these regression models that controlled for F/V (Table 2-8), but there were a few discrepancies. In particular, the summarized values suggest that CPUE of yellow rock crab, the most heavily targeted species along the coast, only decreased by 0.55 crabs per trap (Table 9) whereas controlling for F/V shows that yellow rock crab CPUE actually decreased by 2.72 crabs per trap (Table 5). In the case of sex composition, summary statistics suggest that the probability a landed yellow rock crab was male increased by 3.0% in 2016-17 (Table 9), but controlling for F/V indicates the probability decreased by 4.8% (Table 7-8). The inaccuracy of summarized statistics increased dramatically when combining landed and discarded crabs (Table S11-S12).

3.6 Depth analyses

Regression results revealed that depth strongly influenced species composition of the catch and brown rock crab were less abundant in deeper waters relative to red or yellow rock crab (Table 10). For every foot that depth increased, odds of capturing red rock crab were 1.043 higher compared to brown rock crab at the islands and odds of capturing red or yellow rock crab were, respectively, 1.062 and 1.039 higher compared with brown rock crab along the coast. Regressions also showed that fishers' average trap depth changed between studies, although results were only significant at the level $\alpha = 0.1$ and only at the islands. After controlling for F/V, island fishers placed traps 19.1 feet deeper in 2016-17 than in 2008 ($p = 0.07$), and coastal fishers placed traps 12.7 feet shallower in 2016-17 than in 2008 ($p = 0.11$; Table S13).

3.7 Weight per trap calculations and revenue estimates

Depending on location, fishers caught an average of 1.84–5.29 fewer pounds of rock crab in 2016-17 than in 2008, suggesting that they earned $2.93–$8.45 less per trap in 2016-17.

4. Discussion

Heavily targeted rock crab stocks in the SBC ecosystem experienced significant declines in indicator values from 2008 to 2016-17, suggesting that fishers and managers should consider additional or alternative management strategies. Every targeted stock experienced declines in CPUE, male size, or both, and no stock that was targeted in both time periods experienced increased size or CPUE. Male crab sizes decreased for three of five stocks, translating to a weight reduction of 8–12% per crab (S. Fitzgerald, unpubl. data). Likewise, overall CPUE decreased by 12% at the islands and 27% along the coast. The probability of catching desirable large males also decreased for two stocks, and discard rates, which are costly in time and effort, increased for three stocks, supporting the idea that rock crab are depleted relative to 2008. Males were depleted more heavily than females across all stocks, which can contribute to sperm limitation and reduced reproductive capacity in crab fisheries – although the effects of male-specific fishing practices on crab populations are case-dependent and unknown for CA rock crab (see Hines et al., 2003; Sato et al., 2010; Pardo et al. 2015; Rains et al., 2018). The two larger species (red and yellow) were also depleted more heavily than the smallest species (brown). Together these patterns imply potential continued depletion of the resource. Our findings agree with those of Parker (2003), who found areas fished for rock crabs in southern CA had lower catch rates and smaller crab sizes than adjacent unfished areas. Historical catch records also suggest patterns of serial depletion of rock crab (Fitzgerald et al., 2018). Stock status cannot

be determined for CA rock crab, but our findings are useful nonetheless because best management practices and fishery management law in the United States dictate that management should act based upon the best available scientific information and should not delay action because of uncertainty (CDFW, 2018, MSFCMA, 2007). Overall, our data suggest additional management approaches that account for stock variation should be considered to help moderate depletion and improve fishers' ability to maintain adequate economic returns.

Our results require careful interpretation because of the snapshot nature of the study and because fishery indicators can change for reasons that cannot be directly accounted for in our research design. For example, CPUE decreased more for brown than red rock crab at the islands despite the larger size and presumably higher desirability of red rock crab. Changes in fishing operations, specifically water depths where they were fished, are important to consider when interpreting this finding. Red rock crab are caught in higher abundance as depth increases from 10 to 50 m. Island fishers indicated that they fished deeper in 2016-2017 than 2008 because of lower overall catch rates in shallower areas, thus resulting in a lower CPUE for brown rock crab as they are less abundant in these deeper waters. Additionally, the increase in CPUE for coastal brown rock crab cannot be attributed to increased abundance of brown rock crab. Fishing partners along the coast revealed that they considered brown rock crabs to be an inferior species in 2008 and avoided them at the time, but established a new market for them by 2016-17. As a result, the increase in CPUE was a reflection of new effort within the fishery. Improved marketability, as well as a need to compensate for smaller overall sizes and CPUE for all species, may have also driven the decrease in discard rate for brown rock crabs at the

islands. These examples illustrate how critical it is that future efforts to assess signs of depletion for CA rock crab continue to validate statistical findings using the types of auxiliary information examined here.

Controlling for F/V and discard status in our analyses also improved our ability to interpret results. Summarized values were not fully adequate for accurately assessing indicator changes. Disproportionate sample sizes for individual F/Vs between study periods caused discrepancies between summarized statistics and regression results. For example, the summarized value for yellow rock crab CPUE for all fishers combined in 2016-17 was artificially inflated because the F/V with the highest CPUE for yellow rock in both studies collected much more data in 2016-17 than in 2008. Controlling for F/V removed any bias stemming from disproportionate sample sizes across fishers or locations, and distinguishing between landed and discarded crab was important for avoiding potential misinterpretations as well. For example, a decrease in crab size would not indicate stock decline if there was an influx of smaller (discarded) crabs into the population as a result of a strong recruitment year. Conversely, if size of landed crab decreased, but there was no increase in CPUE of landed or discarded crab, we know trap yields have declined. While landed crabs are what directly impacts fishers, it remains important to examine patterns among discarded crab stocks to help explore whether factors other than fishing (e.g., year class strength) may have been responsible for indicator changes.

Our data do not allow us to distinguish between the effects of intensified fishing and changes in environmental conditions. However, both factors have accurately predicted stock decline in other crab fisheries globally (Kruse et al., 2010), both factors can act synergistically to reduce ecosystem resilience and increase a population's susceptibility to

overexploitation (Harley and Rogers-Bennett, 2004; Ling et al., 2009; Edgar et al., 2010; Sumaila et al., 2011), and both factors likely impacted CA rock crab stocks. Fishing pressure for rock crab in the SBC intensified beginning in 2010 as a result of increased market demand and activation of latent fishing capacity (Fitzgerald et al., 2018), both for the primary fished stocks and species not previously targeted in some areas (*i.e.*, coastal brown rock crab). During this time, a strong El Niño-Southern Oscillation (ENSO) and related warming event also occurred (Huang et al., 2016), and elevated temperatures have been associated with lower productivity in the SBC ecosystem (Holbrook et al., 1997). We detected a weak but significant negative correlation between rock crab landings in the SBC and *in situ* water temperature (Appendix C; CDFW, 2017; CalCOFI, 2017), suggesting reduction in catches could have been influenced by the environmental conditions of the later sampling period. A general lack of information about the effects of warm water on rock crab populations prevents a thorough evaluation of the influence of ENSO on rock crab stocks (although see Appendix C for a discussion on this topic). Nonetheless, intensified fishing in a changing ocean environment has put CA rock crab at potential risk of decline, which warrants the implementation of more active management. Importantly, improved management can lead to increased fishery yields despite negative impacts of warming events (Gaines et al., 2018). Regardless of the underlying mechanisms driving the declines we detected in this study, managers and stakeholders can use our results develop alternative management approaches that protect potentially vulnerable stocks and improve fishers' livelihoods.

Our findings indicate that the fishery is at risk of financial loss. The changes we detected in revenue per trap (section 3.7) translate to financial losses of $11,736 - $84,498

per year if fishers pulled between 100-200 traps per week and worked 40-50 weeks a year. Such estimated losses occurred regardless of season and year. We ignored factors such as increased market availability and slightly increased prices in 2016-17, but these losses remain considerable even with these factors. Further, we may have underestimated stock decline in this study (Appendix D) which would mean these losses could be even higher. Based on our estimates, fishers would need to deploy more traps or pursue alternative livelihoods to maintain a consistent standard of living, something that has happened over the past decade. In fact, the rock crab fishery could become economically unsustainable before populations are biologically overfished (see also Diele et al., 2005), as some fishers exited the fishery despite mean sizes remaining well above the size limit. As such, we recommend that future managerial decisions strongly consider the economic sustainability of the fishery.

Changes in our indicators reflected negative effects for fishers, but not universal resource depletion across the fishery. Instead, the resource impacts we identified occurred at specific locations for specific species and sexes. This outcome illustrates the limitations of managing multiple sedentary, multispecies populations as one aggregate stock. Impacts occurring within the multispecies fishery could be missed if the fishery as a whole is assessed. This shortcoming, however, is useful for highlighting potential ways to improve management of the rock crab fishery. Protecting vulnerable stocks in areas where impacts are being detected while continuing to fish healthy stocks may help ensure long-term sustainability of the resource and increase economic stability for fishers. Specifically, we recommend the development of an adaptive empirical indicator-based

management framework that integrates collaborative data collection and an assessment similar to what we used in this study.

Empirical harvest strategies use indicator assessments to adjust allowable catch or effort according to a predetermined set of simple rules agreed upon by stakeholders and managers. Empirical methods are increasingly incorporated into management strategies of data-rich and data-limited fisheries (Dowling et al., 2015a), and such frameworks can perform as well or better than data-intensive, model-based approaches (Geromont and Butterworth 2014; 2015). For example, Dichmont and Brown (2010) used simple indicator-based decision rules to successfully manage a crab fishery, and Legault et al. (2014) generated catch advice for yellowtail flounder based on a model-free estimate of abundance derived from bottom trawl surveys. The southern CA rock crab fishery has demonstrated successful collection of essential fisheries data, and our regression models could serve as assessment methods in a spatially- and species-specific management strategy for CA rock crab. The only remaining requirement would be for stakeholders and managers to establish rules for adjusting harvest through a collaborative process. Implementing such a system would be cost-effective and more robust than the current system of evaluating landings and other limited data (Culver et al. 2010; Culver et al. 2015; Wilson et al., 2018). The costs of data collection are also negligible compared to the annual losses estimated above, so these practices could pay for themselves if they are translated into improved management over time. However, consideration of the financial impact of our recommendations warrants detailed economic and social analysis that is beyond the scope of this study.

Other potential management options that could be considered, such as setting individual size limits for different stocks or reducing fishery capacity, are limited by a lack of data on size at maturity and fishing effort, and an overall inability to perform reliable model-based stock assessments. These types of static management approaches (e.g., size limits) have also led to poor outcomes for other crab fisheries (Orensanz et al., 1998; Fina, 2005; Salomon et al., 2007) and do not inherently allow for stakeholder involvement or adaptation to new information. Conversely, an adaptive harvest strategy centered upon fisher-collected empirical indicators offers a collaborative opportunity to manage according to the best available information while also reducing uncertainty through iterative learning. Small-scale fisheries research consistently emphasizes the benefits of including stakeholders in the management process (Smith et al., 1999, Pomeroy and Douvere, 2008, Sampedro et al., 2017, and many others), and the simple act of actively managing a fishery with the support of local community partners can improve the sustainability of data-limited fisheries (Hilborn and Ovando, 2014). As such, we strongly encourage collaboration between fishers and managers when developing new or additional management strategies for CA rock crab.

5. Conclusions

The best available science indicates that fishing conditions have worsened in the southern CA rock crab fishery, likely due to increased fishing pressure and ENSO. We have demonstrated that using a relatively simple regression approach to assess empirical indicators can provide valuable insight to managers, even in complex multispecies and spatially structured systems. If used periodically, a collaborative approach based upon at-sea collection of timely, spatially specific data and fishery indicator assessments will

improve management of CA rock crab by increasing the understanding of mechanisms driving stock decline. We suggest that an empirical harvest strategy centered on this approach would be cost-effective and would allow for harvest control rules that account for species, sex, and location. If designed properly, a new harvest strategy would also allow for adaptation to new discoveries, enabling stakeholders and managers to deal with uncertainty and respond to unforeseen changes that adversely affect stock productivity or fishers' livelihoods. Such a strategy is not a panacea for every eventuality, but it provides an appropriate infrastructure for improving the economic and perhaps biological sustainability of the southern CA rock crab fishery. The process we describe promotes adaptive learning, improves communication between stakeholders and managers, and facilitates spatially explicit management of sedentary species in data-limited circumstances. Such methods may be used to improve the monitoring, assessment, and management of other data-limited fisheries worldwide.

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Tables

Table 1. Total numbers of counted (left) and measured crab (right) from both studies. The left column reflects sample sizes used in discard rate analyses; the right column reflects sample sizes used in size and sex analyses. F/V = fishing vessel.

	Sample Size	
	Total number of crabs	Measured crabs
5 F/Vs, 2008	18,958	2,616
Same 5 F/Vs, 2016-17	36,748	6,029
All 7 F/Vs, 2016-17	45,207	7,683

Table 2. Landed crab size (CW, mm) in 2008 vs. 2016-17 for species and sex combinations at the islands. The coefficients tested from Eq. 1 are in the 'Test' column. F = test statistic, df = degrees of freedom, p = p-value, SE = standard error of the size difference, N = sample size. Asterisks indicate a significant difference between years (*p < 0.05, **p < 0.01, ***p < 0.001). Bold font represents a significantly smaller size in 2016-17.

	Test (Eq. 1)	**F (df = 1, 1488)**	**p**	**Size difference, mm (SE)**	**N (number of crabs measured)**
Red Males* **	**$\beta_3 = \beta_2$**	**28.4905**	**< 0.001**	**-8.12*** (1.52)**	**352**
Red Females	$\beta_5 = \beta_4$	1.2721	0.2596	-0.85 (0.75)	590
Brown Males*	**$\beta_7 = \beta_6$**	**4.8021**	**0.0286**	**-4.23* (1.93)**	**80**
Brown Females	$\beta_9 = \beta_8$	0.2432	0.6220	-2.94 (5.96)	40

Table 3. Landed crab size (CW, mm) in 2008 vs. 2016-17 for species and sex combinations on the mainland coast. The coefficients tested from Eq. 2 are in the 'Test' column. df = degrees of freedom, F = test statistic, p = p-value, SE = standard error of the size difference, , N = sample size. Asterisks indicate a significant difference between years (*p < 0.05, **p < 0.01, ***p < 0.001). Bold font represents a significantly smaller size in 2016-17.

	Test (Eq. 2)	**F (df = 1, 7100)**	**p**	**Size difference, mm (SE)**	**N (number of crabs measured)**
Red Males	$\beta_4 = \beta_3$	0.0660	0.7973	-0.72 (2.82)	147
Red Females	$\beta_6 = \beta_5$	3.3157	0.0687	2.70 (1.48)	254
Yellow Males* **	**$\beta_{12} = \beta_{11}$**	**29.5244**	**< 0.001**	**-3.80*** (0.70)**	**1740**
Yellow Females	$\beta_{14} = \beta_{13}$	0.4826	0.4873	-0.37 (0.53)	1705

Table 4. Regression model results of landed crab CPUE from the islands for each species, as well as overall CPUE. The top row represents the coefficient of interest, the change in size in 2016-17 relative to 2008. For model equations, see main text (Eq. 3, 5).

	CPUE (number of crabs per trap)		
	Red	Brown	All Species
β_1 (2016-17)	**-0.299**	**-0.635*****	**-0.942***
	(0.401)	*(0.149)*	*(0.394)*
β_2 (FV1)	0.989^{*}	0.873^{***}	1.842^{***}
	(0.386)	*(0.157)*	*(0.369)*
β_0 (Intercept)	6.001	0.887	6.927
	(0.253)	*(0.067)*	*(0.249)*
$F_{2,750}$	3.353	16.683	14.451
Model p-value	0.037	<0.001	<0.001
Adjusted R^2	0.006	0.053	0.032
Residual Std. Error (df = 750)	5.219	1.995	5.050

Note: n = 753 traps; italicized values are robust standard errors;
**p<0.05; **p<0.01; ***p<0.001*

Table 5. Regression model results of landed crab CPUE from the coast for each species, as well as overall CPUE. The top row represents the coefficient of interest, the change in size in 2016-17 relative to 2008. For model equations, see main text (Eq. 4, 6).

	CPUE (number of crabs per trap)			
	Red	Yellow	Brown	All Species
β_1 (2016-17)	**-2.076^{***}**	**-2.723^{***}**	**0.573^{***}**	**-4.226^{***}**
	(0.243)	*(0.384)*	*(0.049)*	*(0.424)*
β_2 (FV1)	-3.795^{***}	6.072^{***}	-0.043	2.234^{***}
	(0.308)	*(0.608)*	*(0.043)*	*(0.658)*
β_3 (FV2)	-3.429^{***}	7.549^{***}	0.383^{***}	4.503^{***}
	(0.198)	*(0.331)*	*(0.073)*	*(0.362)*
β_0 (Intercept)	5.570	7.984	-0.040	13.515
	(0.316)	*(0.303)*	*(0.029)*	*(0.416)*
$F_{3,1912}$	122.58	187.60	75.51	70.84
Model p-value	<0.001	<0.001	<0.001	<0.001
Adjusted R^2	0.278	0.201	0.062	0.091
Residual Std. Error (df = 1912)	3.297	6.536	1.516	7.025

Note: n = 1,916 traps; italicized values are robust standard errors;
**p<0.05; **p<0.01; ***p<0.001*

Table 6. Coefficient test results from binomial logistic regression showing the difference in probability of discarding a crab by species and location between 2008 and 2016-17. The coefficients tested from Eq. 7 (islands) and 8 (coast) are in the 'Test' column. df = degrees of freedom, χ^2 = test statistic, p = p value, N = sample size. Asterisks indicate a significant difference between periods (*p<0.05, **p<0.01, ***p<0.001). Bold font indicates a significantly higher discard probability in 2016-17. 95% confidence intervals associated with individual coefficients are in Table S8.

	Test (Eq. 7-8)	df	χ^2	p	Difference in discard probability	N (total number of crab caught)
Reds, Islands* **	$\beta_3 = \beta_2$	1, 7975	12.139	< 0.001	**0.027*** **	**6,809**
Browns, Islands**	$\beta_5 = \beta_4$	1, 7975	10.643	0.0011	-0.057**	1,171
Yellows, Coast* **	$\beta_4 = \beta_3$	1, 47684	263.96	< 0.001	**0.102*** **	**39,221**
Reds, Coast	$\beta_6 = \beta_5$	1, 47684	1.789	0.1810	0.018	4,283
Browns, Coast**	$\beta_8 = \beta_7$	1, 47684	10.285	0.0013	**0.242****	**4,188**[a]

[a]*Note: only 42 of these crabs were captured in 2008 because they were not targeted in that year*

Table 7. Coefficient test results from binomial logistic regression showing the difference in probability of landing a male crab by species and location between 2008 and 2016-17. The coefficients tested from Eq. 9 (islands) and 10 (coast) in the main text are in the 'Test' column. df = degrees of freedom, χ^2 = test statistic, p = p value, N = sample size. Asterisks indicate a significant difference between periods (*p<0.05, **p<0.01, ***p<0.001). Bold font indicates a significantly lower male probability in 2016-17. 95% confidence intervals associated with individual coefficients are in Table S8.

	Test (Eq. 9-10)	χ^2	df	p	Difference in probability a landed crab is male	N (number of crabs sexed)
Reds, islands*	$\beta_3 = \beta_2$	6.0871	1, 1496	0.0136	**-0.093***	**942**
Browns, islands	$\beta_6 = \beta_5$	1.6781	1, 1496	0.1952	0.103	120
Reds, coast	$\beta_4 = \beta_3$	2.2861	1, 7112	0.1305	-0.056	401
Yellows, coast*	$\beta_8 = \beta_7$	5.0275	1, 7112	0.0249	**-0.048***	**3,445**

*Note: *p<0.05*

Table 8. Summary of regression results (Table 2-7) for four indicators: size, CPUE, discard rate (probability a crab was landed), and sex composition (probability a crab was male). Results for size, CPUE, and sex are for landed crab only. Red cells (-) indicate a significant decline from 2008 to 2016-17, green cells (+) indicate a significant increase, and gray cells (n.s.) indicate no significant change. Cells are combined according to the specificity of each individual analysis. N/A = not available due to small sample size in at least one period (n < 30). M = male; F = female.

	Islands				**Coast**					
	Red		Brown		Red		Yellow		Brown	
	M	F	M	F	M	F	M	F	M	F
Size	-	n.s.	-	n.s.	n.s.	n.s.	-	n.s.	N/A	
CPUE	n.s.		-		-		-		+	
Probability landed	-		+		n.s.		-		-	
Sex	-		n.s.		n.s.		-		N/A	

Table 9. Summary statistics for the four main indicators without controlling for fishing vessel (F/V). Except for discard rate, calculations are for landed crabs only. Size (mm) and CPUE (crabs per trap) are shown as means (standard error). Discard rate and sex composition are predicted probabilities [95% confidence intervals] that a crab is discarded or male, calculated by removing F/V from Equations 7-10 in the main text. Data are from the same F/Vs in all years (all F/Vs and discarded crabs are included in Table S12). Footnotes indicate small sample sizes where n < 30.

		Size (mm)		CPUE (# per trap)	Discard rate (probability)	Sex composition (probability male)
		Male	Female			
Brown rock crab, islands	**2008**	139.80 *(1.19)*	129.48 *(1.36)*	1.27 *(0.10)*	0.288 [0.260 - 0.317]	0.636 [0.538 - 0.725]
	2016-17	135.60 *(1.53)*	126.62 *(6.65)*	0.80 *(0.10)*	0.196 [0.149 - 0.254]	0.810 [0.589 - 0.927]
Red rock crab, islands	**2008**	171.28 *(0.93)*	144.05 *(0.46)*	6.44 *(0.23)*	0.259 [0.247 - 0.272]	0.420 [0.381 - 0.460]
	2016-17	163.08 *(1.19)*	143.13 *(0.59)*	6.32 *(0.33)*	0.362 [0.342 - 0.382]	0.288 [0.242 - 0.339]
Brown rock crab, coast	**2008**	127.00[a] *(2.40)*	130.27[b] *(4.51)*	0.04 *(0.01)*	0.452 [0.310 - 0.603]	0.500[c] [0.200 - 0.800]
	2016-17	124.31 *(0.81)*	117.16 *(0.63)*	0.81 *(0.05)*	0.741 [0.728 - 0.754]	0.540 [0.463 - 0.616]
Red rock crab, coast	**2008**	152.59 *(1.98)*	139.25 *(0.96)*	3.70 *(0.24)*	0.209 [0.194 - 0.225]	0.399 [0.329 - 0.474]
	2016-17	151.66 *(2.02)*	141.82 *(1.13)*	0.88 *(0.06)*	0.239 [0.218 - 0.261]	0.342 [0.283 - 0.406]
Yellow rock crab, coast	**2008**	141.71 *(0.59)*	125.32 *(0.36)*	11.47 *(0.36)*	0.364 [0.355 - 0.373]	0.482 [0.448 - 0.517]
	2016-17	137.45 *(0.30)*	124.39 *(0.22)*	10.92 *(0.18)*	0.493 [0.487 - 0.499]	0.512 [0.493 - 0.531]

[a] *n = 4;* [b] *n = 4;* [c] *n = 8*

Table 10. Multinomial logistic regression results showing species caught as a function of depth (ft) at the Channel Islands (left) and along the CA coast (right). The model equation is in the main text (Eq. 11) and was applied separately to the two locations. The row in bold indicates the coefficient of interest, the odds ratio (OR) of capturing a given species as depth increases (relative to brown rock crab). Bracketed text = OR 95% confidence intervals. Yellow rock crab at the islands were excluded from this table (n = 1).

	Odds Ratio of landing a certain species		
	Islands	Coast	
	Reds	Reds	Yellows
Depth (ft)***	1.043	1.062	1.039
	[1.036 , 1.050]	[1.055 , 1.068]	[1.034 , 1.044]
Intercept***	0.150	4.136^{-5}	0.024
	[0.084, 0.269]	[1.417^{-5} , 1.207^{-4}]	[0.011, 0.052]
Number of crabs measured	1,036	5,020	399
Nagelkerke's Pseudo R^2	0.306	0.106	
Log Likelihood	-293.071	-2,719.235	
Likelihood Ratio Test χ^2	180.47*** (df = 4)	404.741*** (df = 4)	

Note: n = 415 for coastal brown rock crab; n = 122 for island brown rock crab;
**p<0.05; **p<0.01; ***p<0.001*

Figures

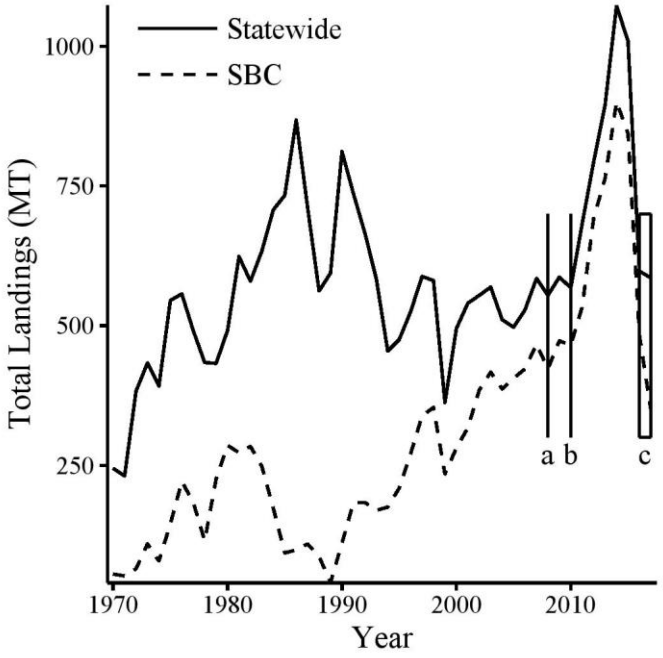


Figure 1. Total catch in rock crab landed (metric tons, MT) from 1970-2017 shown separately for the state of CA combined (solid line) and the Santa Barbara Channel (SBC) only (dashed line). a: 2008 data collection (Culver et al., 2010). b: 2010 management change that activated latent effort creep (permit transferals). c: 2016-2017 data collection (this study).

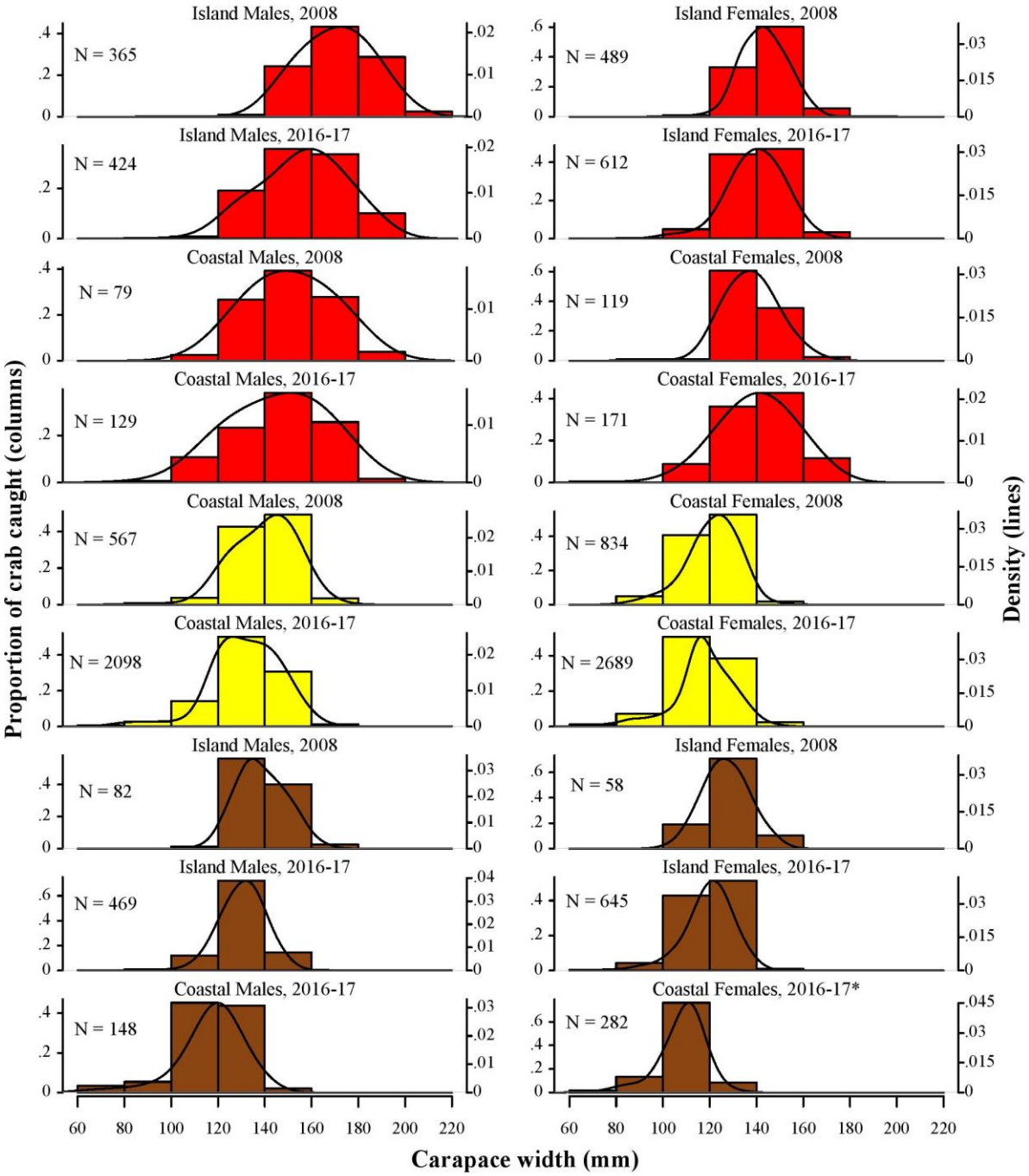


Figure 2. Size distribution of rock crab from the Channel Islands and the mainland CA coast in 2008 and 2016-17, shown via histograms (columns; left y-axis) and density plots (black lines; right y-axis). Columns represent the proportion of rock crab caught for each unique combination of species, sex, location, and study period in 20-mm size classes. Red columns represent red rock crab (top 8 panels), yellow represents yellow rock crab (next 4 panels), and brown represents brown rock crab (bottom 6 panels). N = sample size. Coastal brown rock crab are excluded in 2008 due to small sample sizes.
*One 57.25 mm female brown rock crab was excluded from the figure for aesthetic purposes.

Supplementary Material

The supplementary tables below show complete model outputs for each regression described in the main text. Results include results for both kept and discarded crabs, rather than kept crabs only. Supplementary tables are referenced throughout the main text to indicate which analysis is being referred to in each table. Supplementary figures are described in the main text.

Table S1. Panel regression of size data for each species and sex along the mainland CA coast (left) and at the Channel Islands (right). Model equations are in the main text (Eq. 1 & 2). FV1 refers to different vessels in the models for the coast and islands. Two models are presented for each location, each with a different dummy variable as the reference category (to avoid singularity; abbreviations in main text).

	Size (mm)			
	Coast (ref = YF16T)	Coast (ref = RM08T)	Islands (ref = RF08K)	Islands (ref = BMI08K)
FV1	-1.070	-1.070	-0.438	-0.438
	(0.575)	(0.575)	(0.717)	(0.717)
FV2	-0.664	-0.664		
	(0.647)	(0.647)		
RM08K	40.659***	13.502*	27.106***	31.323***
	(2.035)	(5.591)	(1.064)	(1.533)
RM16K	39.935***	12.778*	18.983***	23.200***
	(2.057)	(5.607)	(1.295)	(1.701)
RF08K	27.418***	0.261		4.217***
	(1.076)	(5.321)		(1.275)
RF16K	30.121***	2.964	-0.847	3.370*
	(1.210)	(5.355)	(0.751)	(1.326)
BM08K	14.746***	-12.411*	-4.217***	
	(2.116)	(5.614)	(1.275)	
BM16K	12.886***	-14.272**	-8.449***	-4.232*
	(0.884)	(5.303)	(1.590)	(1.931)
BF08K	18.008***	-9.149	-14.548***	-10.331***
	(3.975)	(6.546)	(1.428)	(1.797)
BF16K	5.752***	-21.405***	-17.490**	-13.273*
	(0.720)	(5.279)	(5.828)	(5.928)
YM08K	29.824***	2.666		
	(0.722)	(5.264)		
YM16K	26.021***	-1.136		
	(0.461)	(5.250)		
YF08K	13.278***	-13.879**		
	(0.607)	(5.243)		
YF16K	12.912***	-14.245**		
	(0.416)	(5.244)		
RM08T	27.157***		23.789***	28.006***
	(5.252)		(1.653)	(1.980)
RM16T	24.825***	-2.332	24.900***	29.117***
	(2.745)	(5.891)	(1.879)	(2.171)
RF08T	13.330***	-13.827*	-2.628*	1.589
	(2.768)	(5.902)	(1.093)	(1.541)
RF16T	15.700***	-11.457	-0.520	3.697*
	(4.741)	(7.041)	(1.245)	(1.653)
BM08T	-4.312	-31.469***	-9.223***	-5.006
	(4.074)	(6.610)	(2.610)	(2.829)
BM16T	-4.145*	-31.302***	-20.605***	-16.388***
	(1.885)	(5.555)	(0.921)	(1.434)
BF08T	-21.517***	-48.674***	-21.121***	-16.904***
	(0.523)	(5.239)	(2.039)	(2.310)
BF16T	-6.489***	-33.646***	-48.496***	-44.279***
	(0.766)	(5.287)	(0.523)	(1.206)
YM08T	24.546***	-2.611		
	(1.210)	(5.357)		
YM16T	10.122***	-17.035**		
	(0.697)	(5.277)		
YF08T	5.507***	-21.650***		
	(0.755)	(5.266)		

YF16T		-27.157***		
		(5.252)		
Intercept	112.424***	139.581***	144.334***	140.117***
	(0.661)	(5.237)	(0.659)	(1.294)
Observations	7,126	7,126	1,505	1,505
Adjusted R^2	0.473	0.473	0.579	0.579
Residual Std. Error	11.980	11.980	11.585	11.585
	(df = 7100)	(df = 7100)	(df = 1488)	(df = 1488)
F Statistic	256.463***	256.463***	130.288***	130.288***
	(df = 25; 7100)	(df = 25; 7100)	(df = 16; 1488)	(df = 16; 1488)

*Note: Values in parentheses reflect robust standard errors; *p<0.05; **p<0.01; ***p<0.001*

Table S2. Crab size (mm) in 2008 vs. 2016-17 for every combination of species, sex, and discard status, Channel Islands. The coefficients being tested from Eq. 1 are presented in the 'Test' column. F = test statistic, df = degrees of freedom, and p = p-value. Asterisks indicate a significant difference between years (*p < 0.05, **p < 0.01, ***p < 0.001). Bold rows represent a significantly smaller size in 2016-17 relative to 2008.

	Test (Eq. 1)	F (df = 1, 1488)	p	Size difference (mm)
Red Males Kept* **	**$\beta_3 = \beta_2$**	**28.4905**	**< 0.001**	**-8.12**
Red Females Kept	$\beta_5 = \beta_4$	1.2721	0.2596	-0.85
Brown Males Kept*	**$\beta_7 = \beta_6$**	**4.8021**	**0.0286**	**-4.23**
Brown Females Kept	$\beta_9 = \beta_8$	0.2432	0.6220	-2.94
Red Males Discarded	$\beta_{11} = \beta_{10}$	0.2134	0.6442	1.11
Red Females Discarded	$\beta_{13} = \beta_{12}$	1.9978	0.1577	2.11
Brown Males Discarded* **	**$\beta_{15} = \beta_{14}$**	**17.8398**	**< 0.001**	**-11.38**
Brown Females Discarded* **	**$\beta_{17} = \beta_{16}$**	**192.9805**	**< 0.001**	**-27.38**

Table S3. Comparison of male versus female size changes from 2008 to 2016-17, Channel Islands. The coefficients being tested from Eq. 1 are presented in the 'Test' column. F = test statistic, df = degrees of freedom, and p = p-value. Asterisks indicate a significant difference in the magnitude of the size change experienced by males versus females between years (*p < 0.05, **p < 0.01, ***p < 0.001). Bold rows represent a significantly larger decline in size for males compared to females.

	Test (Eq. 1)	F (df = 1,1488)	p	Difference in difference
Reds Kept* **	**$\beta_3 - \beta_2 = \beta_5 - \beta_4$**	**18.3964**	**< 0.001**	**7.28**
Browns Kept	$\beta_7 - \beta_6 = \beta_9 - \beta_8$	0.0423	0.8370	1.29
Reds Discarded	$\beta_{11} - \beta_{10} = \beta_{13} - \beta_{12}$	0.1239	0.7249	1.00
Browns Discarded***	$\beta_{15} - \beta_{14} = \beta_{17} - \beta_{16}$	22.9502	< 0.001	15.99

Table S4. Crab size (mm) in 2008 vs. 2016-17 for every combination of species, sex, and discard status, mainland coast. The coefficients being tested from Eq. 2 are presented in the 'Test' column. df = Degrees of Freedom, F = test statistic, and p = p-value. Asterisks indicate a significant difference between years (*p < 0.05, **p < 0.01, ***p < 0.001). Bold rows represent a significantly smaller size in 2016-17 relative to 2008.

	Test (Eq. 2)	F (df = 1, 7100)	p	Size difference (mm)
Red Males Kept	$\beta_4 = \beta_3$	0.0660	0.7973	-0.72
Red Females Kept	$\beta_6 = \beta_5$	3.3157	0.0687	2.70
Yellow Males Kept* **	**$\beta_{12} = \beta_{11}$**	**29.5244**	**< 0.001**	**-3.80**
Yellow Females Kept	$\beta_{14} = \beta_{13}$	0.4826	0.4873	-0.37
Red Males Discarded	$\beta_{16} = \beta_{15}$	0.1567	0.6922	-2.33
Red Females Discarded	$\beta_{18} = \beta_{17}$	0.1904	0.6626	2.37
Yellow Males Discarded* **	**$\beta_{24} = \beta_{23}$**	**121.7931**	**< 0.001**	**-14.42**
Yellow Females Discarded* **	**$\beta_{26} = \beta_{25}$**	**53.2468**	**< 0.001**	**-5.51**

Table S5. Comparison of male versus female size changes from 2008 to 2016-17, mainland coast. The coefficients being tested from Eq. 2 are presented in the 'Test' column. df = Degrees of Freedom, F = test statistic, and p = p-value. Asterisks indicate a significant difference in the magnitude of the size change experienced by males and females between years (*p < 0.05, **p < 0.01, ***p < 0.001). Bold rows represent a significantly larger decline in size for males relative to females.

	Test (Eq. 2)	F (df = 1, 7100)	p	Difference in difference (mm, absolute)
Reds Kept	$\beta_4 - \beta_3 = \beta_6 - \beta_5$	1.1568	0.2822	3.43
Yellows Kept* **	**$\beta_{12} - \beta_{11} = \beta_{14} - \beta_{13}$**	**18.5447**	**< 0.001**	**3.44**
Reds Discarded	$\beta_{16} - \beta_{15} = \beta_{18} - \beta_{17}$	0.3454	0.5568	4.70
Yellows Discarded* **	**$\beta_{24} - \beta_{23} = \beta_{26} - \beta_{25}$**	**35.7031**	**< 0.001**	**8.92**

Table S6. Multiple regression model results of CPUE data from the Channel Islands for each species and discard status, as well as overall CPUE. The model equations are in the main text (Eq. 3 for the species-specific model, Eq. 5 for the overall model). The row in bold indicates the coefficient of interest, the change in size in 2016-17 relative to 2008. SE = standard error.

	CPUE (number of crabs per trap)					
	Red (Kept)	Red (Discarded)	Brown (Kept)	Brown (Discarded)	All Species (Kept)	All Species (Discarded)
β_1 (2016-17)	**-0.299**	**0.747***	**-0.635*****	**-0.451*****	**-0.942***	**0.270**
	(0.401)	*(0.319)*	*(0.149)*	*(0.087)*	*(0.394)*	*(0.319)*
β_2 (FV1)	0.989*	3.140***	0.873***	0.712***	1.842***	3.851***
	(0.386)	*(0.257)*	*(0.157)*	*(0.099)*	*(0.369)*	*(0.263)*
β_0 (Intercept)	6.001	0.865	0.887	0.200	6.927	1.092
	(0.253)	*(0.111)*	*(0.067)*	*(0.028)*	*(0.249)*	*(0.112)*
$F_{2,750}$	3.353	77.681	16.683	26.069	14.451	108.325
Model p-value	0.037	<0.001	<0.001	<0.001	<0.001	<0.001
Adjusted R^2	0.006	0.178	0.053	0.087	0.032	0.224
Residual SE (df = 750)	5.219	3.557	1.995	1.212	5.050	3.615

*Note: N = 753 traps; Italicized values are robust standard errors; *p<0.05; **p<0.01; ***p<0.001*

Table S7. Multiple regression model results of CPUE data from the mainland coast for each species and discard status, as well as overall CPUE. The model equations are in the main text (Eq. 4 for the species-specific model, Eq. 6 for the overall model). The row in bold indicates the coefficient of interest, the change in size in 2016-17 relative to 2008. SE = standard error.

	CPUE (number of crabs per trap)							
	Red (Kept)	Red (Discarded)	Yellow (Kept)	Yellow (Discarded)	Brown (Kept)	Brown (Discarded)	All Species (Kept)	All Species (Discarded)
β_1 (2016-17)	**-2.076*****	**-0.403*****	**-2.723*****	**1.135****	**0.573*****	**1.312*****	**-4.226*****	**2.045*****
	(0.243)	*(0.086)*	*(0.384)*	*(0.371)*	*(0.049)*	*(0.098)*	*(0.424)*	*(0.381)*
β_2 (FV1)	-3.795***	-1.053***	6.072***	3.800***	-0.043	0.288***	2.234***	3.035***
	(0.308)	*(0.111)*	*(0.608)*	*(0.470)*	*(0.043)*	*(0.062)*	*(0.658)*	*(0.480)*
β_3 (FV2)	-3.429***	-1.147***	7.549***	7.988***	0.383***	2.147***	4.503***	8.988***
	(0.198)	*(0.082)*	*(0.331)*	*(0.379)*	*(0.073)*	*(0.150)*	*(0.362)*	*(0.395)*
β_0 (Intercept)	5.570	1.545	7.984	3.598	-0.040	-0.558	13.515	4.585
	(0.316)	*(0.107)*	*(0.303)*	*(0.262)*	*(0.029)*	*(0.059)*	*(0.416)*	*(0.272)*
$F_{3,1912}$	122.58	86.95	187.60	173.41	75.51	86.62	70.84	207.69
Model p-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Adjusted R^2	0.278	0.194	0.201	0.163	0.062	0.097	0.091	0.202
Residual SE (df = 1912)	3.297	1.223	6.536	8.716	1.516	4.240	7.025	9.122

*Note: N = 1,916 traps; Italicized values are robust standard errors; *p<0.05; **p<0.01; ***p<0.001*

Table S8. Binomial logistic regression results showing the probability of discarding a crab by species and year. Two separate regression models are presented, one for the Channel Islands and one from the mainland CA coast. The model equations are in the main text (Eq. 7 and 8).

	Probability of Discarding a Crab [95% Confidence Interval]	
	Islands	Coast
FV1	0. 776***	0.481***
	[0.754 , 0.796]	[0.461 , 0.500]
FV2		0.559***
		[0.541 , 0.576]
Y08		0.345***
		[0.331 , 0.359]
Y16		0.447***
		[0.429 , 0.465]
R08	0.142**	0.220***
	[0.130 , 0.155]	[0.201 , 0.240]
R16	0.169*	0.238***
	[0.150 , 0.189]	[0.214 , 0.264]
B08	0.135	0.455
	[0.116 , 0.1567	[0.312 , 0.606]
B16	0.078	0.697***
	[0.056 , 0.1078	[0.676 , 0.718]
Sample Size	7,980	47,692
Nagelkerke's *pseudo-R^2*	0.095	0.084
Likelihood Ratio Test (χ^2)	548.9*** (df = 4)	3,099.1*** (df = 7)

Note: Confidence intervals calculated using the modified Wald method; FV1 refers to a different vessel in each model;
**p<0.05 **; p<0.01; ***p<0.001*

Table S9. Binomial logistic regression (BLR) model results for sex composition by species, discard status, and year at the Channel Islands (left) and the mainland CA coast (right). The model equations are in the main text (Eq. 9 and 10).

	Probability of crab being male [95% Confidence Interval]	
	Islands	Coast
FV1	0.257*	0.676***
	[0.213 , 0.306]	[0.635 , 0.716]
FV2		0.704***
		[0.660 , 0.744]
R08K	0.553***	0.249
	[0.502 , 0.603]	[0.190 , 0.320]
R16K	0.460**	0.193
	[0.388 , 0.533]	[0.147 , 0.249]
B08K	0.796***	0.447
	[0.711 , 0.861]	[0.165 , 0.768]
B16K	0.899	0.355
	[0.743 , 0.965]	[0.278 , 0.441]
Y08K		0.384***
		[0.345 , 0.425]
Y16K		0.336***
		[0.295 , 0.380]
R08T	0.653***	0.254
	[0.576 , 0.723]	[0.130 , 0.438]
R16T	0.690***	0.519
	[0.600 , 0.767]	[0.385 , 0.650]
B08T	0.704*	0.715
	[0.551 , 0.822]	[0.213 , 0.959]
B16T	0.810	0.122
	[0.266 , 0.980]	[0.090 , 0.164]
Y08T		0.220*
		[0.187 , 0.257]
Y16T		0.202*
		[0.172 , 0.236]
Sample Size	1,505	7,126
Nagelkerke's *pseudo-R^2*	0.115	0.065
Likelihood Ratio Test (χ^2)	134.016*** (df = 8)	352.028*** (df = 13)

*Note: Confidence intervals calculated using the modified Wald method; *p<0.05; **p<0.01; ***p<0.001*

Table S10. Coefficient test results from binomial logistic regression showing the difference in the probability of capturing a male crab by species, location, and discard status between 2008 and 2016-17. The coefficients being tested from Eq. 9 (islands) and 10 (coast) in the main text are presented in the 'Test' column. df = degrees of freedom, χ^2 = test statistic, p = p value. Bold rows indicate a significantly lower probability of capturing a male crab in 2016-17 than in 2008.

	Test	χ^2	df	p	Difference in probability crab is male
Reds Kept, islands*	**$\beta_3 = \beta_2$**	**6.0871**	**1, 1496**	**0.0136**	**-0.093**
Browns Kept, islands	$\beta_6 = \beta_5$	1.6781	1, 1496	0.1952	0.103
Reds Discarded, islands	$\beta_7 = \beta_6$	0.6170	1, 1496	0.4322	0.037
Browns Discarded, islands	$\beta_9 = \beta_8$	0.2289	1, 1496	0.6324	0.106
Reds Kept, coast	$\beta_4 = \beta_3$	2.2861	1, 7112	0.1305	-0.056
Yellows Kept, coast*	**$\beta_8 = \beta_7$**	**5.0275**	**1, 7112**	**0.0249**	**-0.048**
Reds Discarded, coast*	$\beta_{10} = \beta_9$	4.9963	1, 7112	0.0254	0.265
Yellows Discarded, coast	$\beta_{14} = \beta_{13}$	1.0265	1, 7112	0.3110	-0.018

*Note: * p < 0.05*

Table S11. Summary of regression results for four indicators: size, CPUE, discard rate (shown as % kept), and sex composition (shown as % Male). Red cells (-) indicate a significant decline from 2008 to 2016-17, green cells (+) indicate a significant increase from 2008 to 2016-17, and gray cells (⟋) indicate no significant change between periods. Cells are combined according to the specificity of each individual analysis. N/A = not available due to small sample size in at least one period (n < 30), K = kept, D = discarded, M = male, F = female.

	Islands								Coast											
	Red				Brown				Red				Yellow				Brown			
	K		D		K		D		K		D		K		D		K		D	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Size	-	⟋	⟋	⟋	-	⟋	-	-	⟋	⟋	⟋	⟋	-	⟋	-	-	N/A			
CPUE	⟋	⟋	+		-		-		-		-		-		+		+		+	
% Kept	-				+				⟋				-				-			
% Male	-		⟋		⟋		⟋		⟋		+		-		⟋		N/A			

Table S12. Summary statistics for the four main indicators for all crabs without controlling for fishing vessel (F/V) or discard status (top), and size, CPUE, and sex composition for discarded crabs only (center) and landed crabs only from all 7 F/Vs (bottom) without controlling for F/V. Size (in mm) and CPUE (crabs per trap) are shown as means (standard error). Discard rate and sex composition are the predicted probability [95% confidence intervals] that a crab is discarded or male. Probabilities were calculated by removing the F/V component from Equations 7-10 in the main text. Results include the same F/Vs in 2016-17 and in 2008 unless otherwise noted (+2 F/Vs indicates all 7 vessels). BRC = brown rock crab, RRC = red rock crab, YRC = yellow rock crab.

All crabs

		Size (mm)		CPUE	Discard rate	Sex composition
		Male	Female	(# per	(probability)	(probability
BRC, coast (all crabs)	**2008**	117.39 (4.36)	122.26 (8.73)	0.07 (0.02)	0.4524 [0.3103 - 0.6027]	0.6154 [0.3436 - 0.8302]
	2016-17	117.29 (1.14)	108.1 (0.62)	3.12 (0.17)	0.7412 [0.7276 - 0.7543]	0.3442 [0.3008 - 0.3904]
RRC, coast (all crabs)	**2008**	150.89 (1.92)	137.48 (1.00)	4.67 (0.30)	0.2093 [0.1944 - 0.2249]	0.3990 [0.3331 - 0.4687]
	2016-17	145.7 (1.75)	140.05 (1.20)	1.16 (0.08)	0.23880 [0.2182 - 0.2607]	0.4300 [0.3751 - 0.4867]
YRC, coast (all crabs)	**2008**	139.94 (0.56)	121.32 (0.38)	18.03 (0.60)	0.3636 [0.3545 - 0.3728]	0.4047 [0.3793 - 0.4307]
	2016-17	131.86 (0.33)	117.69 (0.25)	21.55 (0.39)	0.4931 [0.4873 - 0.4989]	0.4383 [0.4243 - 0.4524]
BRC, islands (all crabs)	**2008**	138.6 (1.12)	126.9 (1.21)	1.79 (0.14)	0.2878 [0.2599 - 0.3174]	0.5857 [0.5025 - 0.6643]
	2016-17	134.3 (1.62)	120.4 (8.09)	1.00 (0.11)	0.1963 [0.1490 - 0.2543]	0.7917 [0.5866 - 0.9105]
	2016-17 (+2 F/Vs)	130.5 (0.45)	119.6 (0.41)	6.79 (0.28)	0.4001 [0.3875 - 0.4127]	0.4210 [0.3923 - 0.4502]
RRC, islands (all crabs)	**2008**	170.26 (0.81)	143.30 (0.43)	8.69 (0.33)	0.2590 [0.2465 - 0.2718]	0.4274 [0.3946 - 0.4609]
	2016-17	165.51 (1.05)	143.20 (0.53)	9.90 (0.53)	0.3616 [0.3417 - 0.3820]	0.3388 [0.2981 - 0.382]
	2016-17 (+2 F/Vs)	156.05 (0.87)	139.74 (0.48)	5.86 (0.25)	0.4331 [0.4194 - 0.4468]	0.4093 [0.3797 - 0.4395]

Discarded crabs

		Size (mm)		CPUE	Sex composition
		Male	Female	(# per trap)	(probability male)
BRC, islands (discards only)	**2008**	134.72 (2.62)	122.78 (2.01)	0.51 (0.06)	0.463 [0.319 - 0.615]
	2016-17	123.51 (0.89)	95.4 (N/A)[1]	0.20 (0.04)	0.667 [0.154 - 0.957]
	2016-17 (+2 F/Vs)	126.93 (1.34)	115.48 (0.64)	2.72 (0.15)	0.219 [0.183 - 0.260]
RRC, islands (discards only)	**2008**	167.82 (1.58)	141.32 (0.97)	2.25 (0.15)	0.446 [0.385 - 0.509]
	2016-17	168.80 (1.81)	143.41 (1.13)	3.58 (0.32)	0.446 [0.370 - 0.524]
	2016-17 (+2 F/Vs)	153.78 (1.65)	135.69 (0.99)	2.54 (0.15)	0.435 [0.386 - 0.485]

BRC, coast (discards only)	**2008**	107.78 (4.60)	90.24 (N/A)[1]	0.03 (0.01)	0.800 [0.309 - 0.973]
	2016-17	107.28 (1.87)	104.87 (0.68)	2.31 (0.14)	0.227 [0.181 - 0.281]
RRC, coast (discards only)	**2008**	139.18 (5.50)	125.15 (2.81)	0.98 (0.08)	0.400 [0.231 - 0.597]
	2016-17	136.58 (2.72)	127.43 (4.77)	0.28 (0.03)	0.708 [0.594 - 0.802]
YRC, coast (discards only)	**2008**	136.33 (1.15)	117.47 (0.60)	6.56 (0.30)	0.304 [0.269 - 0.342]
	2016-17	121.56 (0.60)	111.45 (0.35)	10.62 (0.28)	0.347 [0.327 - 0.367]
Landed crabs (not shown in main text)					
BRC, islands (landed only)	**2016-17** (+2 F/Vs)	131.36 (0.44)	124.15 (0.36)	4.07 (0.17)	0.550 [0.512 - 0.587]
RRC, islands (landed only)	**2016-17** (+2 F/Vs)	157.5 (0.94)	141.94 (0.48)	3.32 (0.15)	0.395 [0.358 - 0.433]

[1]N/A values for standard error reflect a sample size of one (N = 1)

Table S13. Regression of trap depth (ft) as a function of year and fishing vessel (F/V) at the Channel Islands (left) and along the CA coast (right). The model equation is in the main text (Eq. 12) and was applied separately to the two locations. The row in bold indicates the coefficient of interest, the change in trap depth in 2016-17 relative to 2008. FV1 and FV2 refer to the two non-reference values of the F/V factor.

	Depth (ft)	
	Islands	Coast
β_1 (2016-17)	19.085^{+}	-12.735
	(10.374)	(7.983)
β_2 (FV1)	7.571	-23.666**
	(7.084)	(7.355)
β_2 (FV2)		-4.753
		(3.548)
β_0 (intercept)	97.344***	188.876***
	(6.642)	(8.074)
Observations	74	240
Adjusted R^2	0.016	0.045
Residual Std. Error	27.44 (df = 71)	24.87 (df = 236)
F Statistic	1.765 (df = 2; 71)	4.073** (df = 3; 236)

Note: Italicized values are robust standard errors;
FV1 refers to a different vessel in each model;
*$^{+}p < 0.1$; *p<0.05; **p<0.01; ***p<0.001*

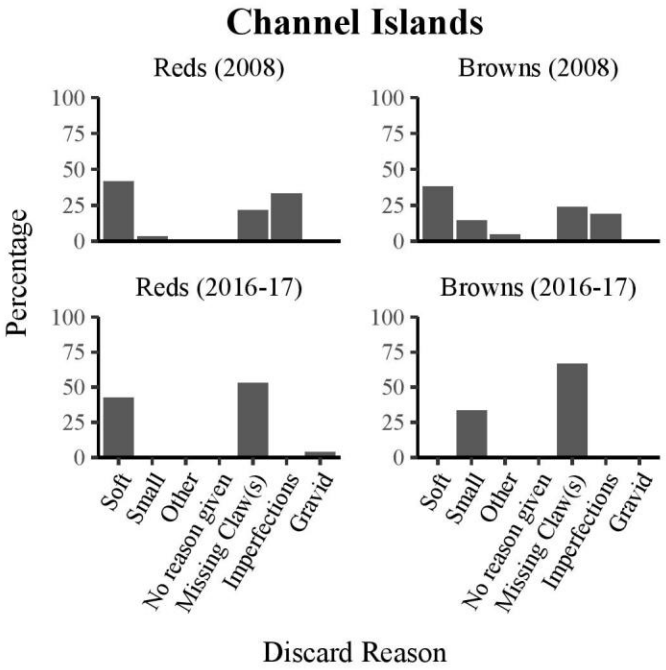


Figure S1. Discard reason for red (left) and brown rock crab (right) in 2008 (top) and 2016-17 (bottom). Chi-squared results showed significant changes for red rock crab (see main text), but not for brown rock crab due to an extremely small sample size of discarded crab in 2016-17 (n = 3).

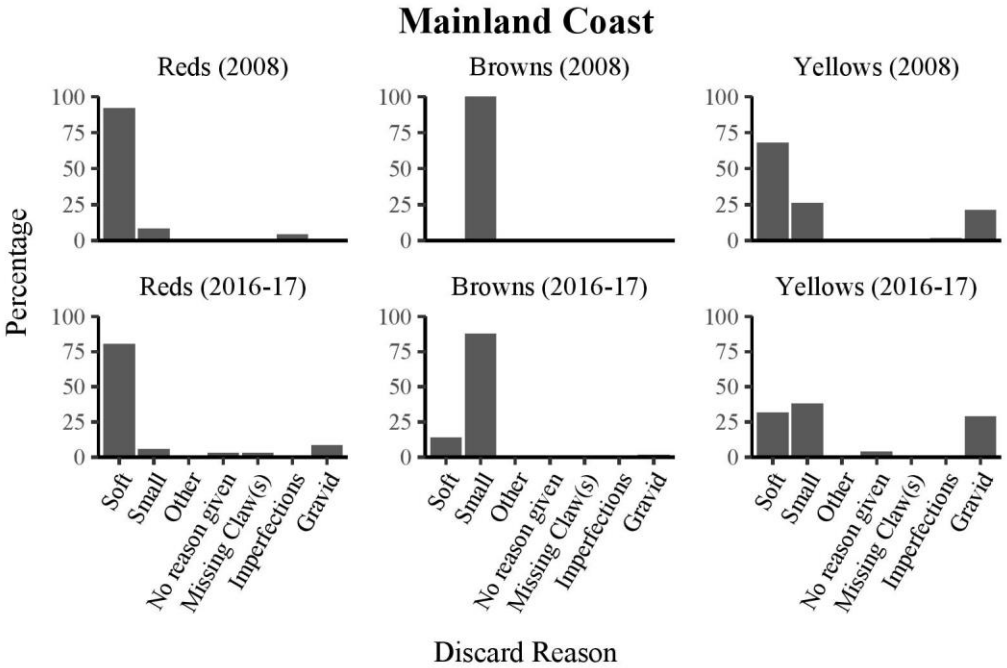


Figure S2. Discard reason for red (left), brown (center), and yellow rock crab (right) in 2008 (top) and 2016-17 (bottom). Chi-squared results showed significant changes for yellow rock crab (see main text) but not the other species, partially due to a small sample size of discarded brown rock crab in 2008 (n = 5).

Appendix A

See supplementary material for field data sheets provided in Appendix A

Appendix B: Sampling protocol provided to fishing partners in this study

ROCK CRAB
COLLABORATIVE AT-SEA SAMPLING PROGRAM (CASP)

2016 PROTOCOL

1. Pull up trap
   If it is the ***first*** trap, fill out the top sections of the "All Traps" datasheet.
   For ***all*** traps, make **note if the trap type or soak time changed from what you recorded on the top of the datasheet**. Other notes of interest should also be recorded (e.g., predation on crab; poaching of trap).

2. Determine if the trap requires detailed data recording (every 5th trap; highlighted row on "All Traps" data sheet)

If it does, skip to step 4a. If it does not go to step 3a.

3a. Remove crabs one at a time. Let deck hand know the species of each crab and whether you will keep it or return it to the sea; have deck hand keep track on the counter.

3b. Once all crabs are removed from the trap and counted, for each species record the total number of crabs kept and returned to sea ("Tossed") on the 'All Traps' data sheet. Don't forget to record '0' if there are no crabs in a certain category.

3c. Proceed to next trap and start back at step #1.

For traps requiring collection of detailed data:

4a. Record the GPS coordinates, trap depth, and any relevant notes (e.g. trap type) on the "All Traps" data sheet.

4b. Follow step 3a, but sort crabs by placing them into separate color coded containers (one for keepers and one for those you will return to sea) as you remove them from the trap.
   'SPECIAL' CIRCUMSTANCE- Molted crabs: If you encounter a soft (freshly molted) crab AND the previous (molted) hard carapace is in the trap, record the size of the soft crab in one row AND the size of the previous shell in the next row. Specify this in the 'Molted' column. See step 4e for measurement instructions.

4c. Follow step 3b.

4d. After you have counted and sorted the crab and recorded number kept/tossed for each species on the 'All Traps' data sheet, reset the counter. Have the deck hand switch to the 'Selected Traps' data sheet.

4e. Pull a crab from one of your sorted containers and have the deck hand record the following on the 'Selected Traps' data sheet:

- The **trap number** the crab came from
- **Species**, **sex**, if it bears **eggs** (female only), and **status** (whether it's being kept or tossed)
- If you will be returning the crab to the sea, record the **reason** it's being returned
- **Size:** using the provided caliper (set to metric – millimeters), measure the carapace width of the crab in the notch between the two farthest back carapace spines (see pictures on back). Be sure to record the entire number provided on the digital readout – do not round the number.

4f. Keep track of how many crab you have measured from each sorted container (keepers and returned for each species) on the counter.

4g. Draw a slash across any blank cells (i.e. 'Eggs' column if male, 'Molted' column for most crab, 'Toss Reason' column if crab is a keeper). You may draw a down arrow through multiple cells to show unchanging information (e.g. trap number for crab from the same trap)

4h. Repeat Steps 4d-4g for each crab until you have measured up to 30 individual crabs **from a single container*** (check the counter as needed). If fewer than 30 crabs are in a container, skip to step 4j. If you reach 30 measured crabs from the same container, move to step 4i.

*Remember, crab are separated by species AND whether they are being kept/tossed. You may have to measure as many as 60 crab of a single species, for example if there are over 30 yellow crab being kept AND over 30 yellows being returned.

4i. If you measure more than 30 crabs from one container, stop doing detailed measurements. Count the remaining crab and enter the number into the Status column.

Example: if there are 37 yellows kept and 32 returned from one trap, write Y in the Species column and 7K, 2T in the Status column.

4j. Record any other notes you think may be of interest about individual crabs or groups of crab.

5. Repeat this process at Step 4d for the other sorted container(s).

6. After all containers have been fully measured and recorded, switch back to the 'All Traps' data sheet and return to step 1.

For the Last 'Select' Trap Serviced (typically trap 70):
Additionally record the time the trap is pulled at the top of the 'Select Traps' data sheet (page 2).

For the Last Trap Serviced (end of your fishing day):

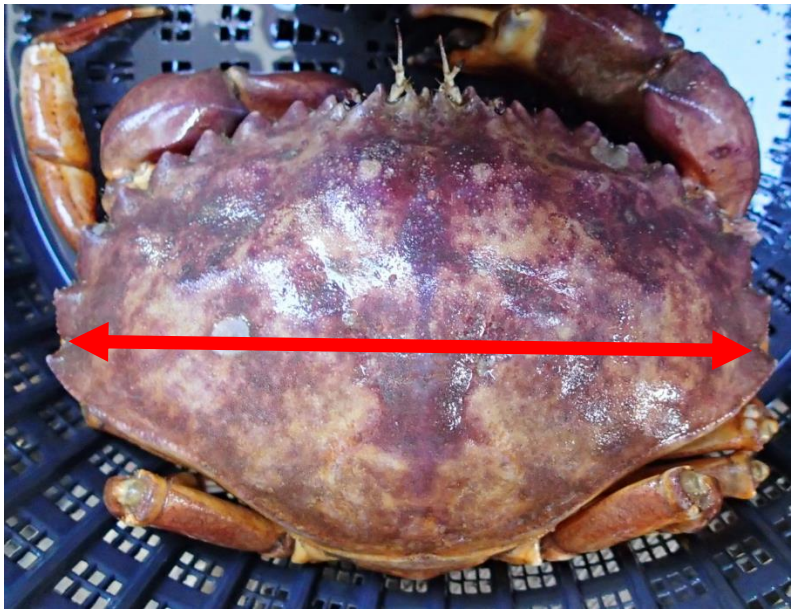
Record the **time, GPS coordinates** and **water depth** for the last trap serviced on the 'All Traps' data sheet.

Sampling Frequency
Sample **once** a month, 3-4 weeks apart.

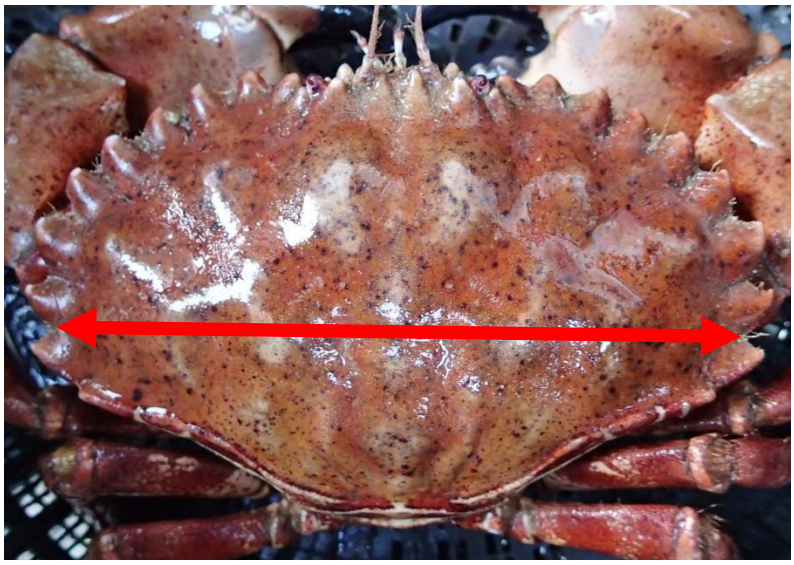
Port Sampling
Port sampling is required for 1-2 of the sampling trips.
The **measured** legal catch will need to be **separated** from the rest of the catch on these sampling days. You will be provided with colored zipties to mark the measured catch.

Red Rock Crab (*Cancer productus*)

Yellow Crab (*Metacarcinus anthonyi*)



Brown Rock Crab (*Romaleon antennarius*)



Appendix C: Potential effects of ENSO-El Niño versus fishing on rock crab populations

The effects of ENSO events on rock crab stocks are uncertain and are probably not universal across species and locations. Cross correlation analysis using the 'ccf' function in R (Stoffer, 2017) revealed a weak but significant correlation between rock crab landings and *in situ* temperature from 1984-2017 (-0.38; CDFW, 2017; CalCOFI, 2017; Fig C.1). However, this analysis was not species- or stock-specific due to unreliable block and species reporting on landing receipts. Temperature correlations with landings were insignificant when using spatially specific landings data from the coast or islands and the same temperature data beginning in 1996 (Fig C.2-C.3). When using a different *in situ* temperature dataset (Reed, 2017) beginning in 2002 (coast) or 2004 (islands), the coast showed a strong negative correlation between landings and temperature on a 1-2 year lag (-0.67, -0.76; Fig C.4), whereas the islands actually showed a positive correlation between landings and temperature on an immediate timescale (0.69; Fig C.5) – although this is probably a coincidental artifact of greatly increased fishing pressure at the islands during a warming period, not a climate-driven effect. Overall, the mechanisms driving these correlations for rock crab in the SBC ecosystem are poorly understood. Warmer temperatures can adversely affect invertebrates by increasing mortality rates, introducing new sources of predation, or reducing maximum sizes and larval settlement, all of which can contribute to lower sizes and CPUE (Leffler, 1972; Sanford, 1999; Lundquist et al., 2000; Caputi et al., 2009; Swiney et al., 2017). Conversely, warmer conditions can lead to increases in CPUE, recruitment, growth rate, juvenile sizes, or abundance for benthic invertebrates, including *Cancer* crabs (Lundquist et al., 2000; del Próo et al., 2003; Oviatt, 2004; Murray and Seed, 2010; Stoner et al., 2010; Mills et al., 2013; Duncombe and

Therriault, 2017). Future efforts such as MPA studies and continued CFR are needed to help disentangle the effects of climate and fishing on CA rock crab (Babcock and MacCall, 2009; Wilson et al., 2010).

Results collectively suggest that the recent ENSO-El Niño event probably had an adverse effect on the rock crab fishery, but multiple lines of evidence suggest that environmental conditions were not the only factor that negatively affected stock health. For example, a 2 year lag suggests that the fishery would not have experienced adverse effects of the 2015-16 ENSO event until 2017, but our model results were similar when assessing 2016 data only. Our results were also unaffected by recruitment-related impacts of the 2015-16 ENSO event because we focused on landed, adult rock crabs and it takes at least two years to reach legal size (Carroll 1982; Carroll and Winn, 1989; Hines 1991; Parker, 2003; Yamada and Groth, 2016). Finally, we expect that warm water events would affect yellow and red rock crab differently because the SBC respectively serves as the northern and southern boundary of their population ranges (Carroll and Winn, 1989). Laboratory experiments also showed that exposure to water temperatures similar to those found in the SBC in 2015-16 increased growth and survival of yellow rock crab (Anderson and Ford, 1976; Anderson, 1978; Reed, 2017) but decreased survival of red rock crab (Sulkin and McKeen, 1994). We therefore consider it a likely sign of fishing-related impacts that both species were depleted in 2016-17 (Table 8, main text). As such, managers and stakeholders should consider the effects of climate on CA rock crab, but they must not ignore the effects of increased fishing pressure on the resource.

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Appendix C Figures

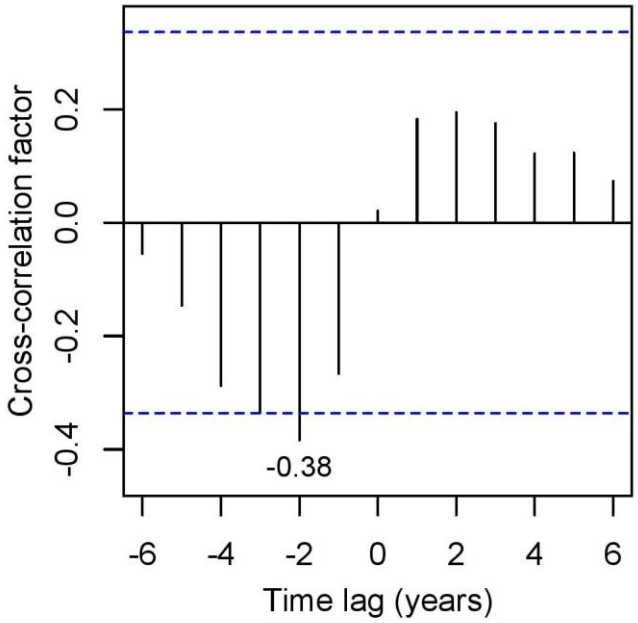

Figure C1. Cross-correlation between water temperature and aggregated rock crab landings in the Santa Barbara Channel (SBC) from 1984-2017 at various time lags. Significant correlations are indicated by a vertical line exceeding the dashed horizontal lines and values for significant correlations at zero or negative lag are indicated below each line.

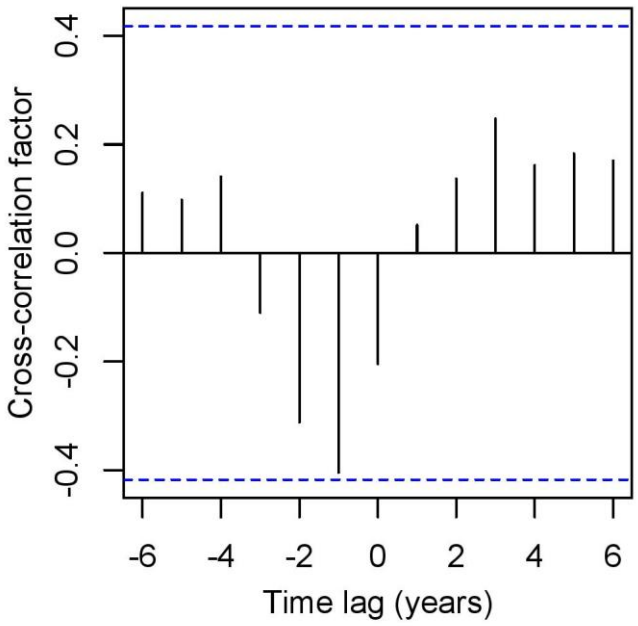

Figure C2. Cross-correlation between SBC water temperature and rock crab landings from the SBC coast at various time lags, 1996-2017. Significant correlations are indicated by a vertical line exceeding the dashed horizontal lines.

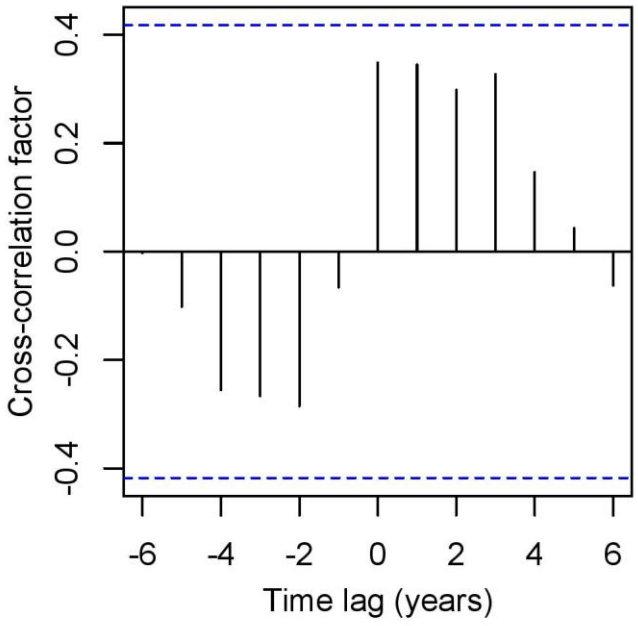

Figure C3. Cross-correlation between SBC water temperature and rock crab landings from the Channel Islands at various time lags, 1996-2017. Significant correlations are indicated by a vertical line exceeding the dashed horizontal lines.

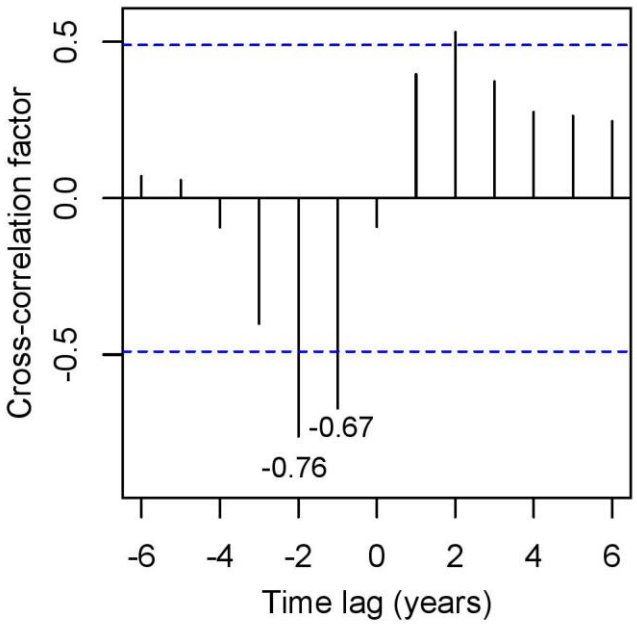

Figure C4. Cross-correlation between Naples Reef water temperature and rock crab landings from the SBC coast at various time lags, 2002-2017. Significant correlations are indicated by a vertical line exceeding the dashed horizontal lines and values for significant correlations at zero or negative lag are indicated below each line.

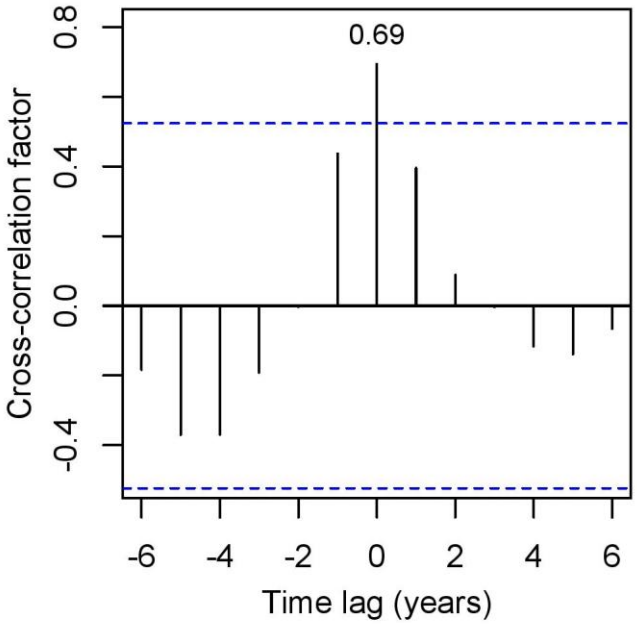

Figure C5. Cross-correlation between Santa Cruz Island water temperature and rock crab landings from the Channel Islands at various time lags, 2004-2017. Significant correlations are indicated by a vertical line exceeding the dashed horizontal lines and values for significant correlations at zero or negative lag are indicated above each line.

Appendix D: Potential for underestimating declines of Channel Island rock crab stocks

Our results may have underestimated levels of stock decline at the Channel Islands. The islands experienced a tremendous increase in fishing pressure from 2010-2015 that was not matched along the coast, so it was surprising that island populations did not show substantially larger signs of decline than coastal populations. Two main factors may have contributed to an underestimation in our results. First, island populations were unfished from November of 2015 until March or June of 2016 (depending on exact location) because of a domoic acid-induced fishery closure (CDFW, 2016; McCabe et al., 2016). This temporary refuge probably resulted in better fishing (i.e., larger sizes and higher CPUE) when the fishery first reopened in 2016, which is when the majority of our island data was collected. Second, our two island fishing partners who participated in both studies quit collecting data by the start of 2017, citing worsening fishing conditions and financial inability to continue participation in the study. Anecdotally, fishing then continued to worsen after they ceased data collection, so we may have detected more severe signs of stock decline had data been collected at the islands throughout 2017. Continued CFR will reduce uncertainty surrounding the accuracy of stock depletion estimates.

Appendix D References

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III. Spillover enhances southern California spiny lobster catch along marine reserve borders following fifteen years of protection

Abstract

No-take marine reserves are effective conservation tools, but their contribution to adjacent fisheries via spillover is less certain. Empirical evidence of spillover for individual reserves does not always match general theoretical predictions. As such, carefully designed site-specific studies are essential for accurately assessing spillover contributions from individual reserves. In 2003, a network of no-take marine reserves was established in California (CA) to conserve biodiversity. The network impacted the Southern CA spiny lobster (*Panulirus interruptus*) fishery, which was considered sustainable at the time, by removing nearly 30% of fishing grounds in the Northern Channel Islands. A collaborative fisheries research (CFR) effort in 2006-08 then detected substantial population increases within reserves, and an indication of possible spillover across reserve borders, using a trap sampling design that controlled for habitat characteristics and other factors. To test for adult spillover 15 years after reserve implementation, I repeated the 2006-08 sampling program in 2018 at two of the three original sampling sites. My objectives were to quantify continued buildup of lobster biomass within the two reserves, and examine whether trap yield increased outside these reserves due to spillover. As in 2006-08, data was collected prior to the fishing season at the same sites located along a gradient from far within reserves to far outside reserve borders. This design removed bias stemming from individual reserve characteristics, fisher behavior, and environmental conditions. Results showed that catch per trap

increased by 125–465% far inside reserves, by 223–331% at sites ≤ 1 km outside reserve boundaries, and did not increase at control sites ≥ 2 km away from reserves. This study is the first to demonstrate enhanced catch near marine reserve borders in the Southern CA spiny lobster fishery, probably due to spillover, and exemplifies that CFR can be used to assess the efficacy of marine reserves as fishery management tools worldwide.

Introduction

No-take marine reserves or Marine Protected Areas (MPAs) are widely recognized as effective conservation tools for protecting the marine resources within their borders (Lubchenco et al., 2003, Halpern et al., 2010; Di Franco et al., 2016; Sala and Giakoumi, 2017). MPAs often lead to increased size and spawning biomass of protected species, which theoretically benefits adjacent fisheries through "spillover" of adults across MPA borders and through increased export of eggs and larvae (Gell and Roberts, 2003; Roberts et al., 2005; Lester et al., 2009; Russ and Alcala, 2011; many others). However, the ability for reserves to benefit adjacent fisheries is controversial (Hilborn et al., 2004, Halpern et al., 2010, Woodcock et al., 2017). MPAs are not guaranteed to meet broader social and environmental objectives, and fishers typically oppose MPA implementation due to the negative impact of reducing the size of available fishing grounds (McClanahan, 1999; Di Lorenzo et al., 2016). Numerous theoretical and empirical studies suggest that reserves benefit adjacent fisheries despite the initial removal of available fishable habitat (*e.g.*, Goñi et al., 2010; Follesa et al., 2011; Kerwath et al., 2013), but empirical evidence does not demonstrate spillover benefits for all reserves (Edgar et al., 2004a; Edgar et al., 2004b; Sale et al., 2005; Forcada et al., 2009; Di Lorenzo et al., 2016). Furthermore, theory suggests that reserves may benefit fisheries only if targeted populations are overfished prior to reserve implementation, in which case only poorly managed fisheries experience reserve benefits (Hilborn et al., 2006; Hart, 2006; Buxton et. al, 2014). The benefits of marine reserves to adjacent fisheries are therefore not universal and depend on the specific context of the fishery and MPA in question.

Marine reserves require ongoing site-specific empirical study to evaluate their long-term success as fishery management tools (Hilborn et al., 2004; Sale et al., 2005; Caselle

et al., 2015; De Leo and Micheli, 2015). However, detecting evidence of spillover is not straightforward. Whether marine reserves benefit fisheries depends on characteristics such as the mobility of the target species (Kramer and Chapman, 1999; Botsford et al., 2003; Abesamis et al., 2006; Le Quesne and Codling, 2009; Gaines et al., 2010; Jiao et al., 2018), the size of the reserve (Gell and Roberts, 2003, Neubert, 2003; Gerber et al., 2005; White, 2009; Lester et al., 2017), and habitat connectivity between the reserve and adjacent fishing grounds (Starr et al., 2004; Forcada et al., 2009; Freeman et al., 2009; Moland et al., 2011). This combination of reserve characteristics is unique for every MPA and fishery, even for MPAs located within the same reserve network (Kay and Wilson, 2012). Broad-scale environmental changes, habitat quality, and fisher behavior can also confound efforts to assess spillover. Many empirical studies demonstrating increased biomass within or near reserve borders lack data from before reserves were implemented or from control sites located far outside reserve borders (reviewed by Halpern, 2003; Lester et al., 2009; Di Lorenzo et al., 2016). Higher biomass in or near reserves may therefore be explained by large-scale environmental changes (*e.g.*, Kerr et al., 2019) or that the best habitat is located within reserve borders (Miller and Russ, 2014). Intense fishing along reserve borders ("fishing the line") can also cause biomass and CPUE to decrease in areas immediately adjacent to reserves (Kellner et al., 2007), so taking snapshot measures of abundance during the fishing season may not accurately reflect spillover. Careful designing studies to control for the above factors is crucial for accurately assessing evidence of spillover.

In 2003, the implementation of an MPA network at the Northern Channel Islands, California (CA), USA removed nearly 30% of available fishing grounds for the southern

CA spiny lobster (*Panulirus interruptus*) fishery, thereby negatively impacting a fishery which was already considered sustainable at the time (CDFG, 2008; Neilson, 2011). Globally, lobster populations within MPAs demonstrate rapid increases in biomass in response to reserve protection, although in many cases the populations were heavily exploited or overfished prior to reserve implementation (e.g., Edgar and Barrett, 1999; Goñi et al., 2006; Goñi et al., 2010; Bevacqua et al., 2010; Follesa et al., 2011; Moland et al., 2013; Ley-Cooper et al., 2014; Thorbjørnsen et al., 2018). In terms of spillover, some studies detected net reserve benefits to lobster fisheries (e.g. Goñi et al., 2010; Kerwath et al., 2013), while others found no spillover evidence of legally-sized lobsters (e.g. Rowe, 2002; Hoskin et al., 2011) or found spillover of only larger, but not more organisms (Thorbjørnsen et al., 2018). To assess the impacts of reserves on southern CA lobster populations, a robust trapping and tagging study was conducted in collaboration with the local lobster fishery from 2006-08 (Kay et al., 2012a; 2012b; Kay and Wilson, 2012). The study controlled for fine-scale habitat features, environmental conditions, and fisher behavior and showed that biomass increased substantially inside reserves. There was also evidence of net emigration of lobsters from inside reserves to adjacent fishing grounds, but any spillover that was occurring had not yet translated to improved fisheries yields. Reserve benefits to the fishery thus remained uncertain at the time (Kay et al., 2012a; 2012b; Withy-Allen and Hovel, 2013). In addition, Before-after-control-impact paired series (BACIPS) analysis found that fishing effort and CPUE for lobster decreased near reserve borders five years after MPA implementation due mainly to the paucity of lobster-rich reef habitat near reserve borders (Guenther et al., 2015). However, a longer time frame (i.e., > 5 yrs) is probably needed to detect and accurately assess spillover

effects for sedentary, long-lived species such as lobsters (Follesa et al., 2011; Kay et al., 2012a), and the original authors cite the need for continued research to measure the extent of spillover for CA spiny lobsters (Kay et al., 2012b).

Anecdotal evidence from fishers suggests that fishing the line at the Northern Channel Islands has greatly increased since 2008, and that catch rates and lobster sizes near reserve borders have increased over time. To test for potential lobster spillover, I partnered with a local fisherman to replicate the previous study by collecting data prior to the opening of the fishing season in 2018 at the same sites sampled by Kay et al. (2012a; 2012b) inside and outside of two Channel Island MPAs. I then assessed spatially explicit changes between 2006-08 and 2018 in catch per trap and size of legally sized CA spiny lobster along a spatial gradient from far inside to far outside the reserves. By 2008, it was already established that CPUE and size of legal lobsters had increased inside reserves and were higher inside reserves than outside (Kay et al., 2012a; 2012b). As such, the focus of this study was not to compare patterns inside versus outside reserves, but rather to assess changes between years within the same locations. I assessed only legally sized lobsters because this study focuses on the use of reserves as a fishery management tool, and catch of sublegal sized lobster is driven by factors other than fishing (Kay et al., 2012b). I quantitatively addressed two main hypotheses: (1) lobster biomass has continued to buildup within MPAs, and (2) fishers are experiencing increased catch per trap outside reserve borders due to spillover. By carefully replicating the previous study and including only preseason data in my analyses, I removed bias stemming from individual reserve characteristics, fisher behavior, and large-scale environmental changes. The robust nature of the prior study design permitted a rare opportunity here to reliably assess empirical

evidence of reserve effects on lobster populations and spillover contributions to the adjoining fishery, thereby meeting a critical need for managers and scientists worldwide to monitor and evaluate the ability of MPAs to achieve their social and ecological objectives.

Methods

Study sites and data collection

Duplicating the original effort described in Kay et al. (2012a; 2012b), I collected size and CPUE data along a spatial gradient from far within MPAs to far outside MPA borders at Scorpion Marine Reserve and Gull Marine Reserve, two no-take MPAs located approximately 30-60 km offshore from mainland CA along the coast of Santa Cruz Island (Fig. 1). The island is one of the Northern Channel Islands found along the southern border of the Santa Barbara Channel in the Southern California Bight, where the state implemented ten no-take marine reserves in April 2003 (CDFG, 2008). A full description of Scorpion and Gull reserve characteristics and sampling site selections is provided in Kay et al. (2012a,b). To summarize, individual trapping sites were selected based on extensive critical habitat surveys and Local Ecological Knowledge (LEK) of commercial fishers. Surveys and LEK ensured that sites were appropriate for lobster sampling based on habitat, historical lobster yield and population size structure, depth, and oceanographic conditions. Traps were placed in the same locations in both studies and were placed ~30 m apart to ensure sample independence. Four trap location categories relative to MPA borders were designated for both reserves: deep inside ("in-deep"), near the inner reserve border ("in-edge"), near the outer reserve border ("out-edge"), and far outside ("out-far"; Fig. 2). Note that "in-deep" refers to location far within reserves and is unrelated to trap depth (i.e., traps at this location were places at the same depths as all other sites).

Trap location designations (in-deep, in edge, out-edge, out-far) were based on trap distance from MPA borders as measured by GPS coordinates, fisher LEK of areas with contiguous habitat, and the spatial scale of lobster movement. Tagging studies over a two-year period (2007-2008) at the Channel Islands showed that most lobsters tagged at the Channel Islands moved ≤ 1 km from their initial tagging site and lobsters rarely moved ≥ 2 km from their initial tagging site (CDFG, 2008, Kay and Wilson, 2012). As such, I defined out-far sites as ≥ 2 km outside a reserve border and out-edge sites as ≤ 1 km outside a reserve border for both MPAs. Inner site designations slightly differed. At Gull, in-deep traps were those set ≥ 2 km inside the western reserve border (where the remainder of trap sampling took place; see Fig. 2). However, traps were only ≥ 0.87 km inside the eastern reserve border, which was not considered in the original study because it was not actively targeted until 2012. All but seven traps remained ≥ 1 km inside the eastern border. In-edge traps were set ≤ 1 km inside the western border of Gull. At Scorpion, there is a sandy beach located ~0.65-0.85 km inside the reserve that disrupts continuous rocky reef habitat. As such, in-deep traps were set ≥ 0.85 km inside the reserve border and in-edge traps were set ≤ 0.65 km inside the reserve border. Fisher LEK supported these designations while at sea. Figure 2 shows the coordinates and categorizations for each trap. Traps with erroneous GPS recordings (i.e., GPS appeared outside of known sampling locations or GPS did not match at-sea trap location designation) and traps that did not closely overlap between the two studies were removed from both datasets.

Traps were set under the guidance of a commercial fisherman in August and September of 2018, just prior to the opening of the commercial and recreational lobster

fishery. Data from the 2006-08 study was restricted to traps set in August and September as well. Traps were identical to those used in the commercial lobster fishery, with the exception that escape ports for sublegal lobsters were closed in order to obtain a fuller representation of population size structure. Complete details regarding commercial trap construction and deployment are described in Kay et al. (2012a). For every trap, I recorded depth, GPS coordinates, date, soak time (number of nights a trap was left in the water), number of lobsters caught, and trap location designation. I also recorded the sex of every lobster caught in every trap, and measured and recorded every lobster's carapace length (CL; mm) to the nearest two decimal points using Mitutoyo 500-763-10 IP67 Absolute Coolant Proof Calipers. While docked inside Scorpion, we also measured lobster weight to the nearest 0.02 kg using a Gempler's digital hanging scale (# 227658) for a subset of lobsters (n = 114) that covered the size spectrum for both sexes sampled in this study. All lobsters were kept shaded when possible to reduce stress and were released in their original location.

Standardizing data for soak time

An important difference between the 2006-08 and 2018 studies was the number of nights a trap was left in the water (soak time). Our own at-sea observations, fisher LEK, and Kay et al. (2012b) show that soak time significantly affects trap CPUE at the Channel Islands, and traps soaked for far fewer nights in this study (1.9 ± 0.8 nights, mean ± SD) compared to 2006-08 (4.5 ± 1.6 nights; Welch's $t_{(df = 1729.6)} = 47.202$, $p < 0.0001$). As such, data required standardization to account for soak time. Modeling efforts suggested that the nature of the relationship (*i.e.*, linear or nonlinear) between soak time and catch per trap varied depending on the number of nights soaked, perhaps due to trap saturation

occurring after multiple nights. The significance and magnitude of soak time's influence on catch per trap was also specific to different combinations of trap location and year (Appendix A1 and Table A1-A2 provide model details and further explanation). I therefore assessed the effect of soak time separately for each combination of year (2006-08 or 2018), MPA (Gull or Scorpion), and trap location (in-deep, in-edge, out-edge, out-far) using the equations

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster) = \beta_0 + \beta_1 Soak + \varepsilon, \quad \text{(Eq. 1)}$$

and

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster) = \beta_0 + \beta_1 Soak + \beta_2 (Soak)^2 + \varepsilon, \quad \text{(Eq. 2)}$$

where β_0 is the intercept, *Soak* is a continuous variable representing the number of nights a trap was left in the water, the $(Soak)^2$ term in Eq. 2 allows for a nonlinear relationship between soak time and catch per trap, β_1 and β_2 are the regression coefficients on *Soak* and $(Soak)^2$, respectively, and ε is an error term describing variance not explained by the regression.

When a model demonstrated a significant relationship between soak time and catch per trap for a given year-MPA-location combination, the best performing model (Eq. 1 or 2) was selected based on AIC and R^2 values. Raw data entries were then standardized to represent the average value for a 3-night soak (the median soak time across all data) by multiplying each data entry by the ratio

$\frac{3\_night}{i\_night}$, where 3_night is the model-predicted value for a 3-night soak and i_night is the model-predicted value for the actual number of nights soaked for the given trap (1-8 nights). When catch per trap was not significantly affected by soak time (*i.e.*, $p > 0.05$ for β_1 in Eq. 1, $p > 0.05$ for β_1 or β_2 in Eq. 2), raw data was not standardized. Linear and

nonlinear model results assessing soak time for each year-MPA-location combination are in Appendix A2 (Table A3-A10). In rare cases where model diagnostics suggested similar fits for linear and nonlinear models, the more conservative data transformation was applied (*i.e.*, data was adjusted to a lesser degree). CPUE (numbers) and weight per trap data (lbs) was standardized for 7 of 16 year-MPA-location combinations, which changed mean catch per trap values by 15-48% (Appendix A2; Tables A11-A12).

Data analysis

I assessed changes in catch per trap from 2006-08 to 2018 in terms of CPUE (numbers per trap) and weight per trap (lbs) of legally sized lobsters using two-sample hypothesis testing for each combination of MPA and trap location (e.g., Gull in-deep CPUE in 2006-08 = Gull in-deep CPUE in 2018). Data for most year-MPA-location combinations exhibited non-normality, skewness, and unequal variances between sites and years regardless of log- or square root transformation, so we used Welch's t-test approximation to compare groups and used untransformed data to provide the simplest possible interpretation of test results. Welch's test is more reliable than other two-sample hypothesis testing methods when variances are unequal (*i.e.*, Student's *t*-test, Mann–Whitney *U*; Zimmerman et al., 1993; Ruxton, 2006), and was the most robust method when comparing samples similar to ours in terms of unequal levels of skewness, variance, and sample size (the true significance level was within 10-20% of the nominal significance value; Fagerland and Sandvik 2009). Finally, type I error rates of Welch's test ($\alpha = 0.05$) were low ($\leq 8\%$) with sample sizes similar to ours even when dealing with highly uneven sample sizes and sample variances as well as data coming from a lognormal, beta, or exponential distribution (Algina et al., 1994).

I also assessed differences in the length frequency of lobster populations sampled from each location using two-sided Kolmogorov-Smirnov (KS) tests. Tests were performed on data combining legal and sublegal lobsters in order to assess the full size structure of the population, but additional tests were performed using only legally sized lobsters in order to provide consistency with catch per trap analyses. When two-sided KS tests revealed a significantly different size distribution between years for a given site ($p < 0.05$), I used one-sided KS tests and the cumulative distribution functions for the two years to determine which sample had a higher proportion of large lobsters.

For all analyses, data was combined for the three early years (2006, 2007, 2008) because there was no significant difference in size or catch per trap of legal lobsters in those years (Kay et al., 2012b). Weights were calculated for each lobster based on sex-specific length-weight observations recorded in this study (S. Fitzgerald., unpubl. data) using the allometric growth equation

$$Wt = a(CL)^b, \quad \text{(Eq. 3)}$$

where *Wt* refers to lobster weight (kg), *CL* refers to lobster carapace length (cm), *a* is a constant and *b* is an allometric scaling parameter. Weights were then converted to pounds (the metric used in the lobster fishery) prior to data standardization for soak time (see above). I generated scatter plots for CPUE and weight per trap data to visualize the assessed differences between year-MPA-location combinations, box-and-violin plots to more accurately visualize the data spread for both variables, and histograms with superimposed density plots to visualize size data. All analysis and figure generation was performed in R (R core team, 2018).

Results

CPUE

Table 1 summarizes Welch's *t*-test results comparing CPUE between years for each combination of MPA and trap location. From 2006-08 to 2018 at Gull, the mean number of lobsters caught per trap increased by 9.5 lobsters at in-deep sites (a 124% increase; $p < 0.001$) and by 1.5 lobsters at out-edge sites (223% increase; $p < 0.001$), whereas mean CPUE decreased by 0.8 lobsters per trap at out-far sites (69% decrease; $p < 0.001$). At Scorpion, mean CPUE increased by 20.5 lobsters per trap at in-deep sites (402% increase; $p < 0.001$), by 7.2 lobsters at in-edge sites (384% increase; $p < 0.001$), and by 1.6 lobsters at out-edge sites (315% increase; $p < 0.001$). CPUE did not change at in-edge sites at Gull or at out-far sites at Scorpion ($p > 0.05$ for both). Figure 3 shows mean CPUE (± SEs) for each year-MPA-trap location combination, and Figure 4 visualizes the data spread for each combination.

Weight

Table 2 summarizes Welch's *t*-test results comparing lobster weight per trap (lbs) between years for each combination of MPA and trap location. From 2006-08 to 2018 at Gull, the mean weight of lobsters caught per trap increased by 26.0 pounds at in-deep sites (a 144% increase; $p < 0.001$) and by 2.8 pounds at out-edge sites (258% increase; $p = 0.001$), whereas mean weight per trap decreased by 1.5 pounds at out-far sites (74% decrease; $p < 0.001$). At Scorpion, mean weight per trap increased by 53.4 pounds at in-deep sites (465% increase; $p < 0.001$), by 13.5 pounds at in-edge sites (335% increase; $p < 0.001$), and by 3.22 pounds at out-edge sites (331% increase; $p < 0.001$). Weight per trap did not change for in-edge sites in Gull or out-far sites at Scorpion ($p > 0.05$ for

both). Figure 5 shows mean weight per trap (± SEs) for each year-MPA-trap location combination, and Figure 6 visualizes the data spread for each combination.

Size

At Gull, KS tests showed that the size distributions of lobster populations (sublegals and legals combined) differed between years for all four sites (Table 3; Fig 7). There was a higher proportion of large lobsters in 2018 at in-deep, in-edge, and out-edge sites, and a smaller proportion of large lobsters in 2018 at out-far sites (one-sided $p < 0.001$ in all cases). These results remained similar when restricting the analysis to legal lobsters only ($p < 0.05$ in all cases; Table 3). At Scorpion, KS tests showed that the size distributions of lobster populations (sublegals and legals combined) differed for in-edge, out-edge, and out-far sites ($p < 0.05$), but not for in-deep sites ($p = 0.07$; Table 3). There was a higher proportion of large lobster at out-edge sites in 2018 (one-sided $p = 0.01$), but a lower proportion of large lobsters in 2018 at in-edge and out-far sites (one-sided $p < 0.01$ for both; Table 3). When restricting analyses to legally sized lobsters, findings remained similar at in-edge and out-far sites (one-sided $p < 0.01$ for both) but were insignificant at the out-edge site ($p > 0.05$; Table 3).

Discussion

Fishing the line at both Gull and Scorpion marine reserves in 2018 resulted in significantly increased catch relative to 2006-08. Mean weight per trap, which is the most appropriate metric for measuring fishery-relevant changes because it accounts for number and size of lobsters, more than tripled ≤ 1 km outside reserve borders at Gull and more than quadrupled at Scorpion. Mean weight per trap also increased within reserves to varying degrees depending on reserve and trap location. Weight per trap at Scorpion

increased by 4.3-5.6 times at in-edge and in-deep sites, respectively ($p < 0.001$ for both), and increased by 0.9-2.4 times at Gull, although the increase at the in-edge site was not significant at the $\alpha = 0.05$ level ($p = 0.06$). Conversely, weight per trap at sites located ≥ 2 km outside reserve borders either significantly decreased (Gull; $p < 0.001$) or showed no significant change (Scorpion). These patterns indicate spillover contributions to the Southern CA lobster fishery. If the substantial increases in preseason weight per trap were a result of broad-scale environmental changes, landings would have uniformly increased across the fishery. However, trap yield did not increase at control sites, confirming that increased weight per trap in and near reserve borders was a reserve-based effect. The direction and significance of results also remained the same when using raw data not standardized for soak time (see Tables A11-A12). Using a collaborative approach, I detected substantial levels of spillover occurring in the Channel Islands CA spiny lobster fishery 15 years after reserves were established. The magnitude of the spillover may have significant economic implications for the fishery, which future research efforts can assess. The approach taken exemplifies the site-specific empirical study needed to assess the efficacy of individual marine reserves as fishery management tools over time.

The roughly fourfold increase in weight per trap of lobsters caught by fishing the outer edge of reserves reflects a considerable contribution of MPAs to the adjacent fishery. Accordingly, at-sea observations from the last week of sampling confirmed that fishers are taking advantage of spillover by placing high numbers of traps near reserve borders (*i.e.*, fishing the line), contrary to fisher behavior in 2008 (Guenther et al., 2015). The true magnitude of spillover benefits experienced by local fishers may also be higher

than estimated here because August and September are months where spiny lobster at the Channel Islands are not particularly mobile. CA spiny lobsters appear to undergo offshore-nearshore migrations beginning in late October, and winter storms cause increased movement rates as well (Kay et al., 2012a; CDFG, 2004; CDFW, 2013). Fishers then move their traps further offshore later in the fishing season to take advantage of these migrations (CDFW, 2013), representing an additional opportunity to benefit from spillover. Substantial fishery enhancement may also be occurring via egg and larval spillover, a key component of MPA benefits to surrounding fisheries that we did not consider in this study (Guénette et al., 1998; Botsford et al., 2009). Finally, the 144–465% increase in weight per trap deep within reserves augments a previously detected four- to eightfold increase in trap yield at these same sites between 1998-2002 and 2007-2008 (Kay et al., 2012a), suggesting that biomass levels deep inside reserves in 2018 may be approximately twenty times pre-reserve levels.

A twentyfold increase in lobster biomass is larger than that detected in most empirical literature (e.g. Follesa et al., 2011; Jack and Wing, 2010; Moland et al., 2013), but is within expected ranges for reserves that have been protected for over fifteen years (Kelly et al., 2000; Shears et al., 2006). However, results from this study are novel because stock assessment determined that the CA spiny lobster fishery was sustainable from 2000 onwards (Neilson, 2011). The increased trap yield at out-edge sites also occurred despite a reported 34% increase in fishing effort (number of traps pulled) in the ten fishing blocks closest to Santa Cruz Island from 1998-2003 to 2013-2017 (CDFW, 2019). To my knowledge, this is the first study to document dramatic reserve-driven increases in trap

yield outside MPA borders in a fishery that was already considered sustainable prior to MPA implementation.

This study provides a robust empirical assessment of CA spiny lobster spillover, but we cannot determine whether the level of spillover we detected offsets the initial costs of losing approximately one-fifth of the viable fishing grounds at the Channel Islands (Kay et al., 2012a; Guenther et al., 2015). MPAs are often promoted to fishing communities as devices that will lead to increased long-term yields, but this advocacy can sometimes be unqualified and misleading, which can cause fishers to have negative perceptions of reserves and lead to friction between fishers, scientists, and managers (Agardy et al., 2003; Hilborn et al. 2004; Bennett and Dearden, 2014). Individual reserves therefore must be monitored and evaluated over time to maintain credibility and transparency between managers and stakeholders (Hilborn et al., 2004). For CA spiny lobster, the next challenge is to assess the overall benefit spillover has on the fishery based on the information generated in this study. Despite the need for continued research, this study remains vital as it demonstrates at least partial success of MPAs as a fishery management tool for CA spiny lobster, and builds upon a strong foundation for monitoring and evaluating reserve success over the long term.

Conclusions

MPA literature consistently calls for the empirical study of individual marine reserves, as theoretical models cannot capture the full complexity of site-specific dynamics that influence whether a given reserve will contribute to a fishery via spillover. This study takes advantage of a robust study design that controlled for important fine-scale habitat features, broad-scale environmental changes, and fishing activity in order to compare catch per trap five and fifteen years after reserve implementation. Future

research will be needed to fully evaluate the impacts of MPA implementation on Southern CA lobster, but empirical results clearly showed that lobster populations have continued to grow inside two Channel Islands MPAs and that adult spillover resulted in increased spiny lobster trap yield at the beginning of the 2018-2019 fishing season. Presenting results as easily digestible means ± SEs and collaborating with local fishers also fostered improved relationships and increased transparency between fishers, scientists, and managers. Establishing and repeating such carefully designed empirical studies is critical for learning whether individual MPAs are meeting fishery-related objectives worldwide.

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Tables

Table 1. Catch-per-unit-effort (CPUE; number of lobsters per trap) for each combination of year, MPA, and trap location, including the difference between years and the associated 95% confidence interval (95% CI) as well as two-sided Welch's *t*-test results comparing CPUE between years. *t* is the test statistic, df = degrees of freedom, and *p* is the p-value. Bold text indicates sites with significantly greater CPUE in 2018 versus 2006-08. N denotes sample sizes in number of traps pulled.

MPA	Trap Location	Mean CPUE, 2008	Mean CPUE, 2018	Mean difference (CPUE) [95% CI]	*t*	df	*p*	N (2008)	N (2018)
Gull	**In-deep**	**7.65**	**17.15**	**9.50 [7.76 - 11.25]**	**-10.73**	**192.63**	**< 0.0001**	**178**	**112**
	In-edge	4.62	6.75	2.13 [-1.27 - 5.53]	-1.27	40.85	0.212	263	40
	Out-edge	**0.66**	**2.13**	**1.47 [0.86 - 2.08]**	**-4.86**	**41.35**	**< 0.0001**	**226**	**40**
	Out-far	1.16	0.35	-0.80 [-1.05 - -0.56]	6.41	308.87	< 0.0001	221	93
Scorpion	**In-deep**	**5.11**	**25.66**	**20.55 [16.9 - 24.19]**	**-11.30**	**54.26**	**< 0.0001**	**35**	**43**
	In-edge	**1.87**	**9.07**	**7.19 [5.45 - 8.94]**	**-8.17**	**87.19**	**< 0.0001**	**39**	**61**
	Out-edge	**0.52**	**2.16**	**1.64 [1.1 - 2.19]**	**-5.97**	**151.74**	**< 0.0001**	**71**	**122**
	Out-far	2.35	2.37	0.02 [-1.12 - 1.16]	-0.03	48.42	0.973	26	52

Table 2. Lobster weight (wt) per trap (lbs) for each combination of year, MPA, and trap location, including the difference between years and the associated 95% confidence interval (95% CI) and two-sided Welch's *t*-test results comparing wt per trap between years. *t* is the test statistic, df = degrees of freedom, and *p* is the p-value. Bold text indicates sites with significantly greater wt per trap in 2018 versus 2006-08. N denotes sample sizes in number of traps pulled.

MPA	Trap Location	Mean wt per trap (lbs), 2006-08	Mean wt per trap (lbs), 2018	Mean difference (lbs) [95% CI]	*t*	df	*p*	N (2008)	N (2018)
Gull	**In-deep**	**18.06**	**44.04**	**25.99 [21.53 - 30.45]**	**-11.50**	**175.13**	**< 0.0001**	**178**	**112**
	In-edge	9.01	17.24	8.23 [-0.42 - 16.88]	-1.92	40.03	0.062	263	40
	Out-edge	**1.08**	**3.87**	**2.79 [1.57 - 4.01]**	**-4.62**	**40.69**	**< 0.0001**	**226**	**40**
	Out-far	2.03	0.54	-1.49 [-1.93 - -1.06]	6.78	298.35	< 0.0001	9	16
Scorpion	**In-deep**	**11.48**	**64.86**	**53.38 [42.83 - 63.93]**	**-10.16**	**49.65**	**< 0.0001**	**221**	**93**
	In-edge	**4.04**	**17.58**	**13.54 [9.97 - 17.11]**	**-7.53**	**90.13**	**< 0.0001**	**35**	**43**
	Out-edge	**0.97**	**4.19**	**3.22 [2.11 - 4.33]**	**-5.73**	**148.51**	**< 0.0001**	**39**	**61**
	Out-far	4.14	4.03	-0.11 [-2.25 - 2.04]	0.10	45.90	0.921	71	122

Table 3. Kolmogorov-Smirnov (KS) test results comparing length frequencies of lobsters between years for each combination of MPA and trap location. *D* is the test statistic, *p* is the p-value, 'Test' indicates whether the results are for a one-sided or two-sided test, 'CDF interpretation' refers to a comparison of the cumulative distribution functions (CDFs) between years to determine which year yielded larger lobsters, and N denotes sample size (number of lobsters measured) in each year. The top panel presents results from analyses that included all lobsters, whereas the bottom panel presents results from analyses restricted to only legal lobsters. Bold text indicates a significantly higher proportion of large lobsters in 2018, whereas asterisks and italic text indicates a significantly smaller proportion of large lobsters in 2018.

All lobsters (legal + sublegal combined)							
MPA	**Trap Location**	***D***	***p***	**Test**	**CDF interpretation**	**N (2008)**	**N (2018)**
Gull	**In-deep**	**0.174**	**< 0.0001**	**one-sided**	**Larger lobsters in 2018**	**2252**	**1705**
	In-edge	**0.264**	**< 0.0001**	**one-sided**	**Larger lobsters in 2018**	**2808**	**389**
	Out-edge	**0.189**	**< 0.0001**	**one-sided**	**Larger lobsters in 2018**	**811**	**175**
	Out-far	*0.169***	*0.001*	*one-sided*	*Smaller lobsters in 2018***	*1064*	*151*
Scorpion	In-deep	0.083	0.067	two-sided	N.S.	311	1156
	In-edge	*0.231***	*< 0.0001*	*one-sided*	*Smaller lobsters in 2018***	*101*	*723*
	Out-edge	**0.148**	**0.012**	**one-sided**	**Larger lobsters in 2018**	**125**	**530**
	Out-far	*0.179***	*0.004*	*one-sided*	*Smaller lobsters in 2018***	*128*	*265*
Legal lobsters only							
MPA	**Trap Location**	**D**	**p**	**Test**	**CDF interpretation**	**N (2008)**	**N (2018)**
Gull	**In-deep**	**0.237**	**< 0.0001**	**one-sided**	**Larger lobsters in 2018**	**579**	**429**
	In-edge	**0.375**	**< 0.0001**	**one-sided**	**Larger lobsters in 2018**	**380**	**99**
	Out-edge	**0.187**	**0.012**	**one-sided**	**Larger lobsters in 2018**	**66**	**57**
	Out-far	*0.251***	*0.022*	*one-sided*	*Smaller lobsters in 2018***	*187*	*17*
Scorpion	In-deep	0.096	0.111	two-sided	N.S.	127	492
	In-edge	*0.232***	*0.001*	*one-sided*	*Smaller lobsters in 2018***	*45*	*156*
	Out-edge	0.180	0.159	two-sided	N.S.	36	157
	Out-far	*0.260***	*0.002*	*one-sided*	*Smaller lobsters in 2018***	*61*	*67*

Figures

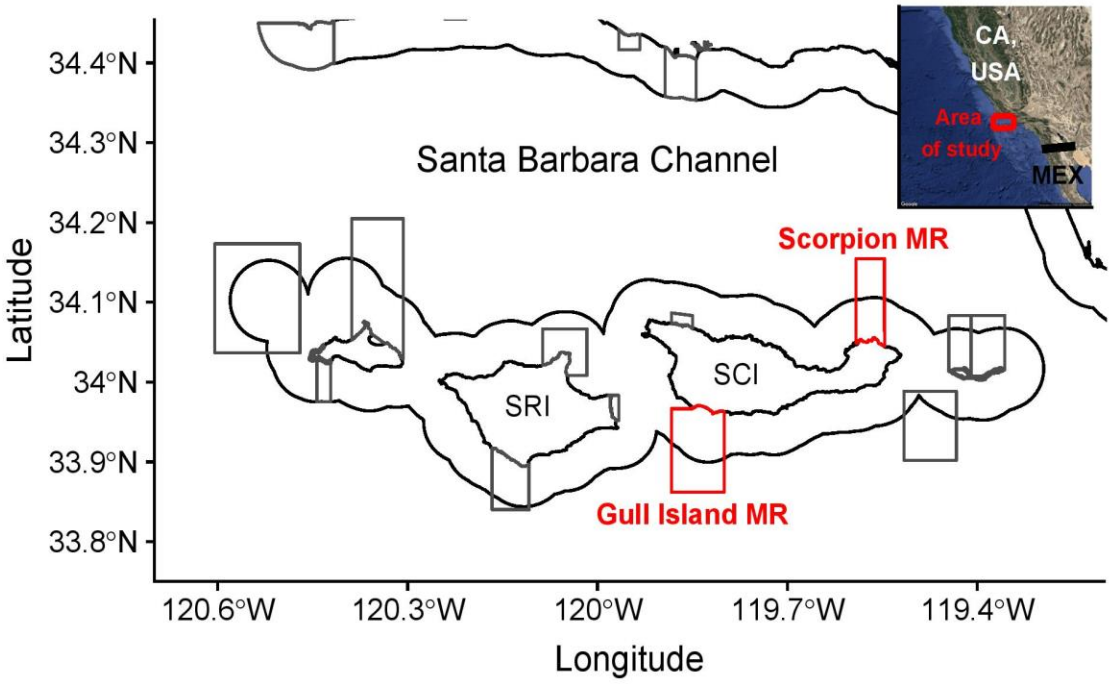

Figure 1. Map showing the study area in the Southern California Bight, including the Santa Barbara Channel and the Northern Channel Islands. Black lines indicate the coast and the state boundary 3 nautical miles offshore. The two largest islands are labeled (SRI = Santa Rosa Island, SCI = Santa Cruz Island). Rectangles (dark gray) represent marine reserves; the reserves sampled in this study (Scorpion, Gull Island) are highlighted in red.

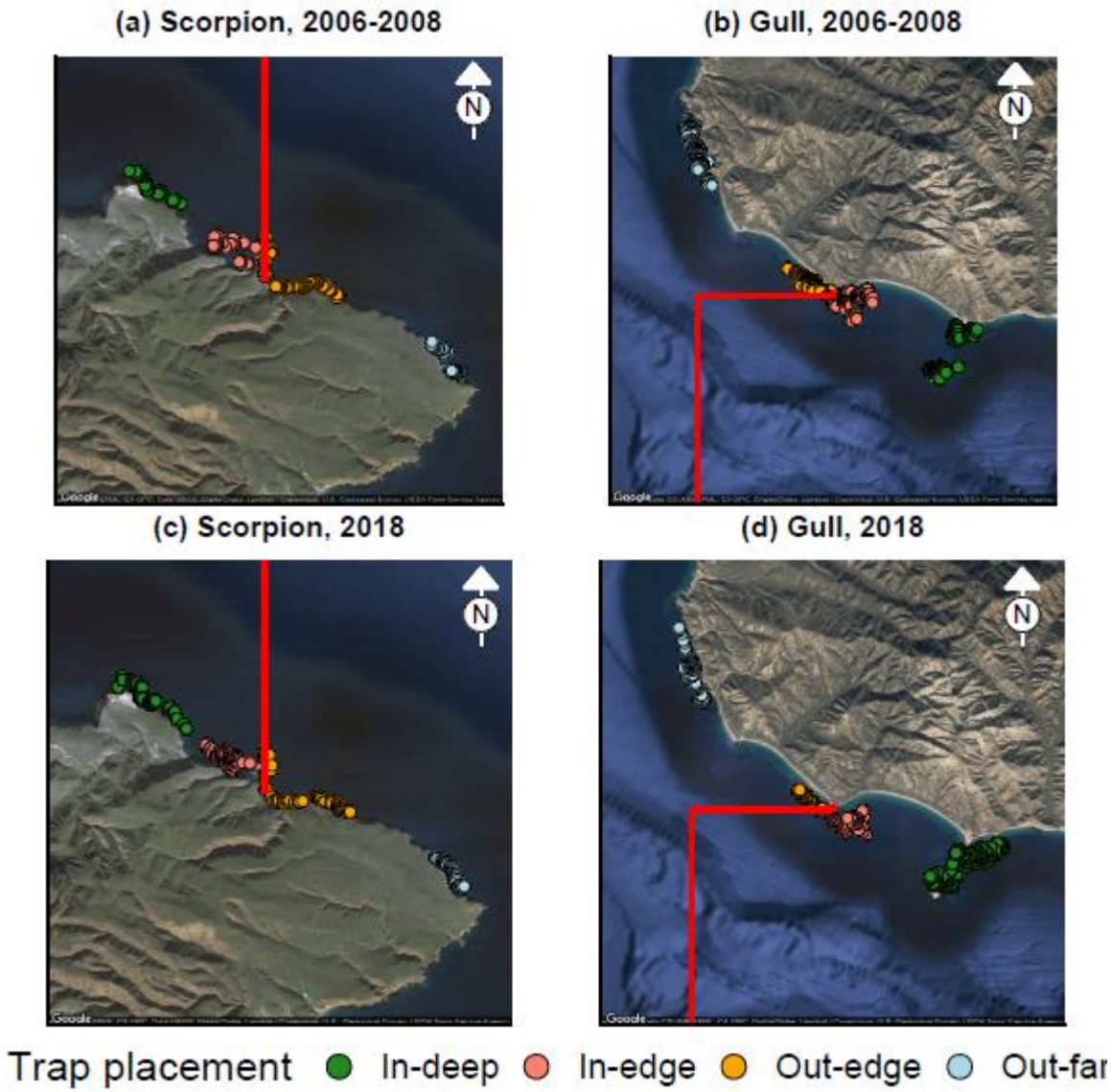

Figure 2. Map showing location of each trap pulled relative to the reserve border (red) for a) Scorpion MPA in 2006-2008 (top left), b) Gull MPA in 2006-2008 (top right), a) Scorpion MPA in 2018 (bottom left), and d) Gull MPA in 2018 (bottom right). Circle colors represent trap location designation (green = in-deep, salmon = in-edge, orange = out-edge, light blue = out-far).

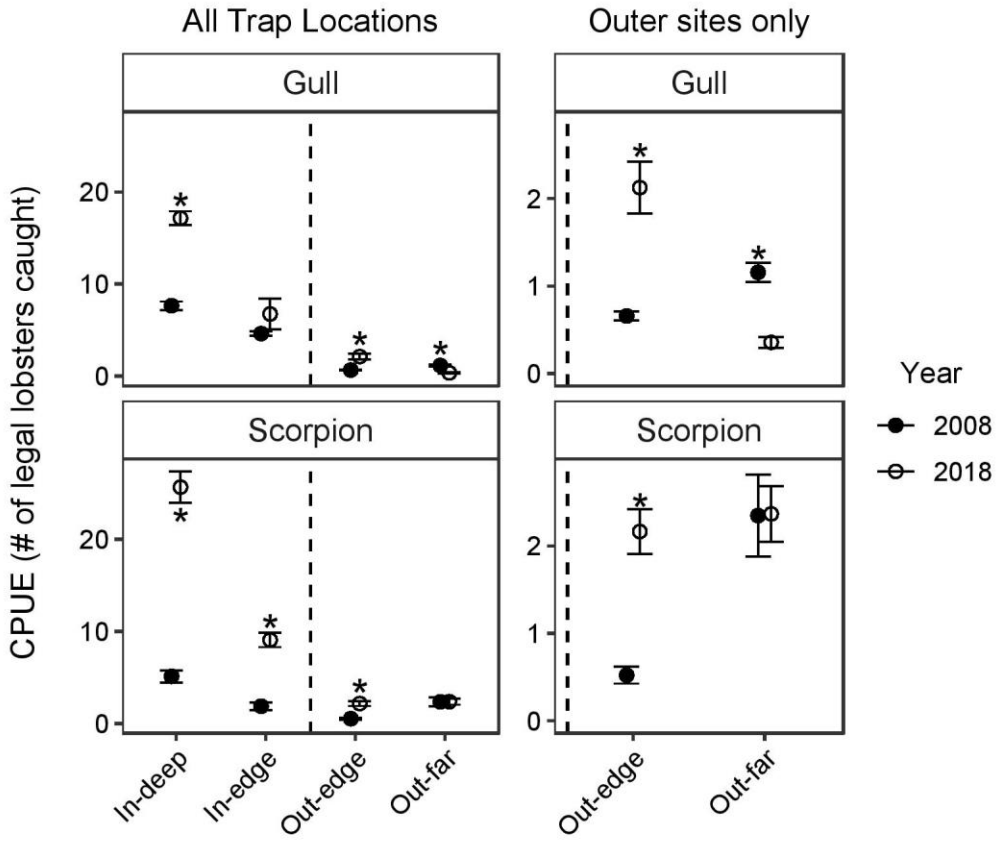

Figure 3. Mean catch-per-unit-effort (CPUE, number of lobsters per trap) for every combination of year, reserve, and trap location. Open circles represent 2018 data, closed circles represent 2006-08 data ("2008"), and error bars represent standard errors. The left panel shows data for all four trap location designations, whereas the right panel zooms in to show only data from sites outside reserves. Asterisks next to a point indicate a significantly higher CPUE for that given year as determined by Welch's t-test; *p<0.05; **p<0.01; ***p<0.001.

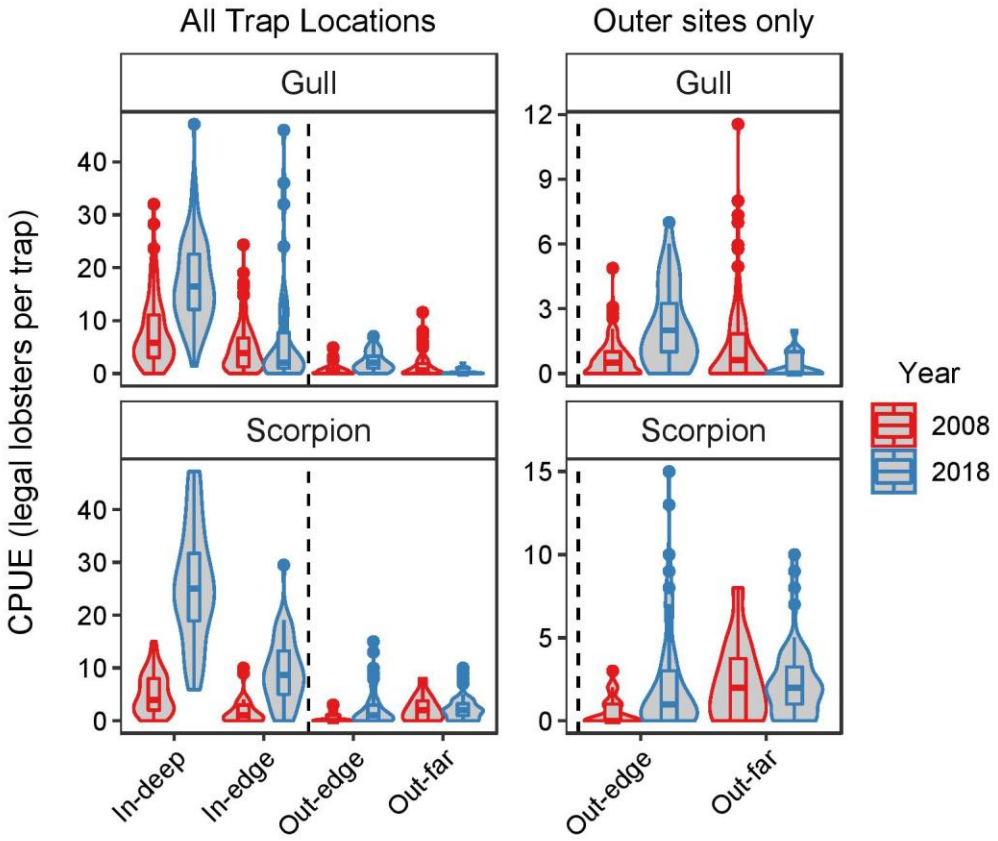

Figure 4. Box-and-violin plot showing the distributions of catch-per-unit-effort (CPUE; number of lobsters per trap) data for every combination of year, reserve, and trap location. Red indicates 2006-08 data ("2008") and blue indicates 2018 data. The box encloses the first and third quartiles, horizontal lines represent median CPUE values, vertical lines represent maximum (top) and minimum (bottom) CPUE values that are not outliers, and points represent outliers. The violin plot encloses the full data spread. The left panel shows data for all four trap location designations, whereas the right panel zooms in to show only data from sites outside reserves.

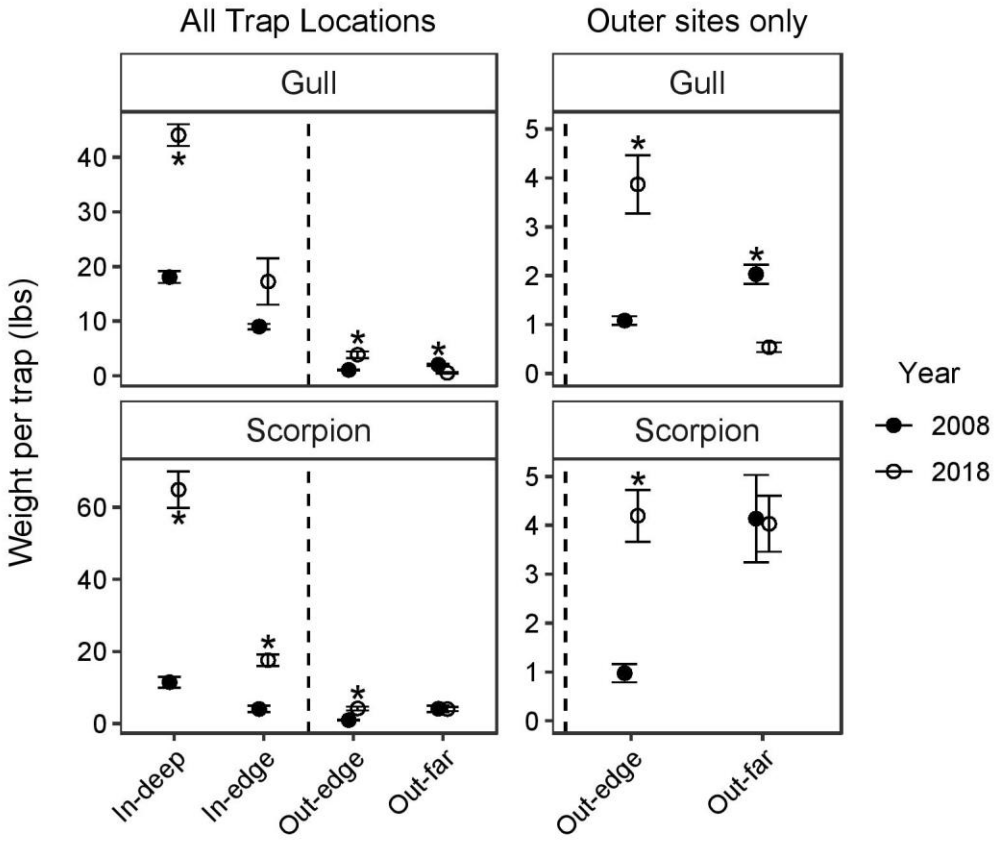

Figure 5. Mean lobster weight per trap (lbs) for every combination of year, reserve, and trap location. Open circles represent 2018 data, closed circles represent 2006-08 data ("2008"), and error bars represent standard errors. The left panel shows data for all four trap location designations, whereas the right panel zooms in to show only data from sites outside reserves. Asterisks next to a point indicate a significantly higher CPUE for that given year as determined by Welch's t-test; *p<0.05; **p<0.01; ***p<0.001.

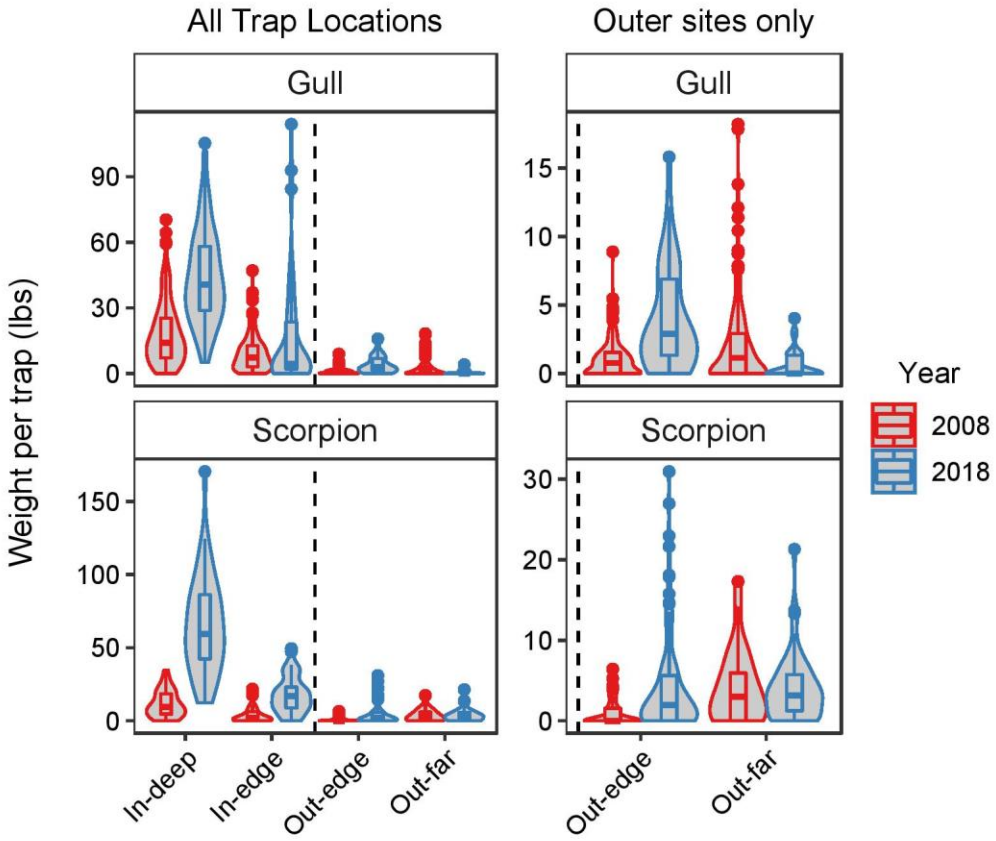

Figure 6. Box-and-violin plot showing the distributions of lobster weight per trap (lbs) data for every combination of year, reserve, and trap location. Red indicates 2006-08 data ("2008") and blue indicates 2018 data. The box encloses the first and third quartiles, horizontal lines represent median weight per trap values, vertical lines represent maximum (top) and minimum (bottom) weight per trap values that are not outliers, and points represent outliers. The violin plot encloses the full data spread. The left panel shows data for all four trap location designations, whereas the right panel zooms in to show only data from sites outside reserves.

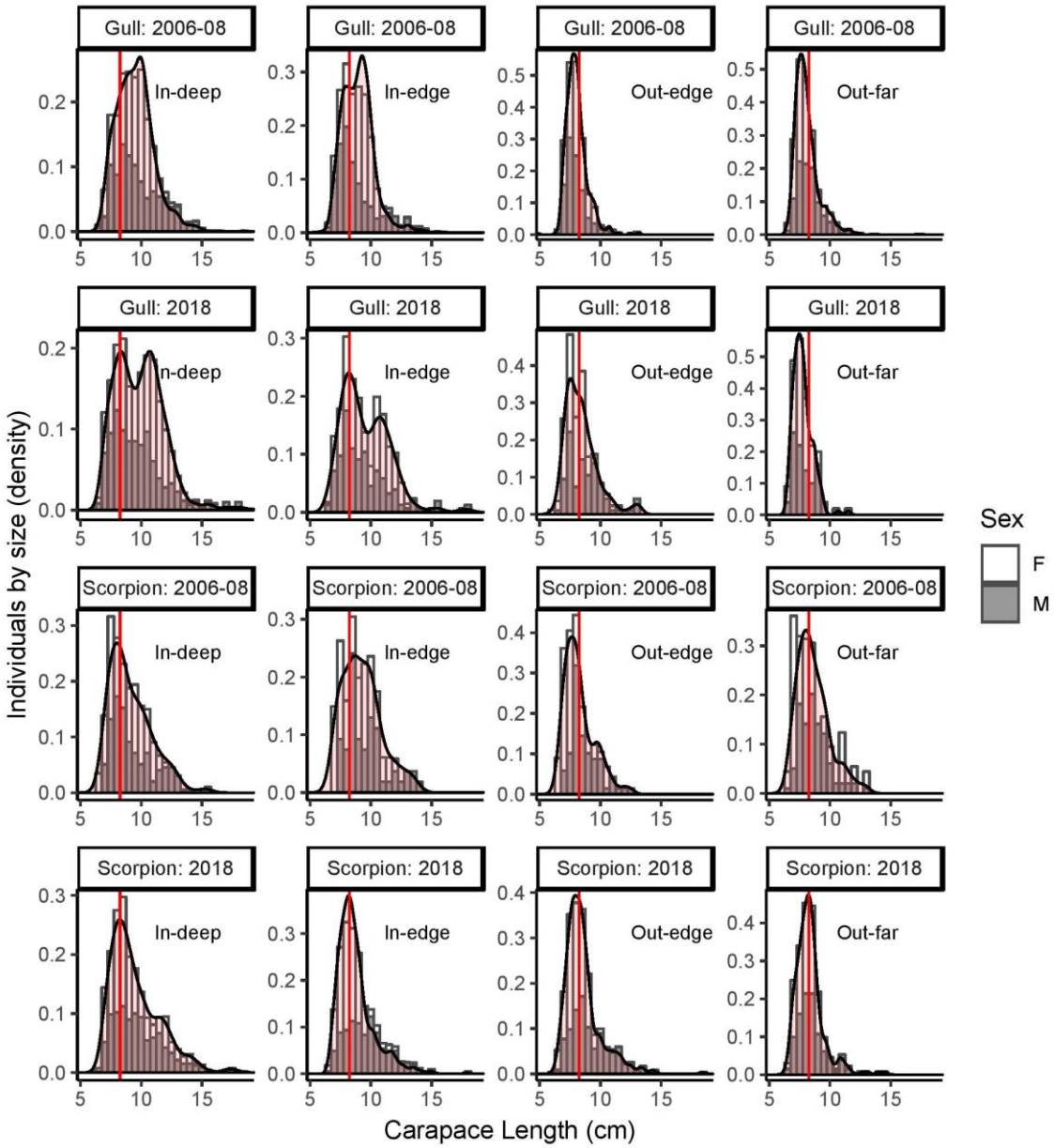

Figure 7. Length frequency (carapace length, cm) of sampled lobster populations for each combination of year (1st and 3rd row = 2006-08, 2nd and 4th row = 2018), reserve (top two rows = Gull; bottom two rows = Scorpion), and trap location (from left to right: in-deep, in-edge, out-edge, out-far). Males are shown in dark gray and females are shown in white. Rectangles indicate histogram bins and lines with pink shading reflect density plots for both sexes combined.

Appendix A: Standardizing data for soak time

Appendix A1: Modeling overall relationship between soak time and catch per trap

General approach

Our observations suggested that the nature of the relationship between soak time and catch per trap may change with the number of nights soaked. For example, at-sea we detected a greater difference between a one vs. three-night soak than a two vs. four-night soak, indicating a nonlinear relationship after the first 1-3 nights as trap saturation may begin to occur. The relationship between soak time and catch per trap may therefore differ between study periods (2006-2008 vs. 2018) because just 4 of 638 traps soaked for longer than three nights in this study, whereas the majority of traps (766 out of 1,115) pulled by Kay et al. (2012a,b) soaked for four nights or more. Furthermore, soak time may not influence catch per trap the same way at all sites as traps may become saturated at some locations but not others. Means and variances also differed dramatically between trap locations and study periods, so applying a uniform data standardization to all sites and years was inappropriate. To mathematically test whether the relationship between soak time and catch per trap differed between years, trap locations, and individual reserves, we modeled the relationship between soak time and catch per trap using the equation

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster) = \beta_0 + \beta_1 Soak + \beta_2 Year + \beta_3 MPA + \beta_4 Dist + \beta_5 Soak * Year * MPA * Dist + \varepsilon \quad \text{(Eq. A.1)}$$

where β_0 is the intercept, *Soak* is a continuous variable representing the number of nights a trap was left in the water, *Year* is a two-level factor referring to time period (2006-2008 or 2018), *MPA* is a two-level factor denoting the individual reserve (Gull or Scorpion), *Dist* is a four-level factor referring to a trap's location relative to the reserve (in-deep, in-

edge, out-edge, or out-far), and *Soak*Year*MPA*Dist* is the four-way interaction of the independent variables. All other β values are model coefficients, and ε is the error term describing variance not explained by the regression.

Model results showed a highly significant interaction between soak time and year for both CPUE (numbers) and weight per trap (lbs) ($p < 0.001$; Table A1), meaning the relationship between soak time and catch per trap varied by year (2006-2008 vs. 2018). Significant interactions were also found for soak and in-edge sites ($p < 0.0001$; Table A1), meaning that the relationship between soak time and catch per trap also varied by trap location in some cases. In this model, the interaction was insignificant for soak:MPA ($p > 0.05$). However, these model results, the rationale explaining why the relationship between soak time and catch per trap may be year and site-specific, and the fact that I use two sample hypothesis testing to assess changes separately for each trap and reserve location, suggest that separate regressions fit to each site and year will provide the most accurate adjustment to account for soak time.

I also assessed both linear and nonlinear model fits for each study period because of the potential that the nature of the relationship between soak time and catch per trap differed between studies. Using the equations

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster)_y = \beta_{0y} + \beta_{1y}Soak + \beta_{2y}MPA + \beta_{3y}Dist + \varepsilon \quad \text{(Eq. A.2)}$$

and

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster)_y = \beta_{0y} + \beta_{1y}Soak + \beta_{2y}(Soak)^2 + \beta_{3y}MPA + \beta_{4y}Dist + \varepsilon, \quad \text{(Eq. A.3)}$$

where variables are the same as above and the *y* subscript denotes the years of study (2006-2008 or 2018), it was determined that a linear model provided a better fit in 2018 for both weight per trap and CPUE data (Table A2), and a nonlinear model fit provided a

better fit for 2006-2008 data (Table A2). As such, I fit both linear and nonlinear models to each year-MPA-location combination and selected the most suitable regression model based on model diagnostics as described in the main text. All analyses were performed in R (R core team, 2018) and all tables were generated using the 'stargazer' package (Hlavac, 2018).

Table A1. Model results from Eq. A.1 showing the overall relationship between soak time and weight per trap (lbs; left) and CPUE (# lobsters per trap; right), including significant interactions in bold.

	Overall soak time model	
	Weight per trap (lbs)	CPUE (# lobsters per trap)
Soak	-0.045 (-0.567)	0.118 (-0.252)
Year2018	-8.381* (-3.816)	-5.036** (-1.695)
MPAScorpion	-13.083* (-5.441)	-5.301* (-2.417)
In-edge	-16.495*** (-3.571)	-6.472*** (-1.586)
Out-edge	-20.397*** (-3.64)	-8.345*** (-1.617)
Out-far	-20.524*** (-3.668)	-8.588*** (-1.629)
Soak:Year2018	**10.361*** (-1.517)**	**4.267*** (-0.674)**
Soak:MPAScorpion	0.758 (-1.134)	0.202 (-0.504)
Year2018:MPAScorpion	16.586* (-7.565)	8.065* (-3.36)
Soak:In-edge	**1.920* (-0.751)**	**0.842* (-0.333)**
Soak:Out-edge	0.196 (-0.76)	-0.029 (-0.338)
Soak:Out-far	0.42 (-0.763)	0.127 (-0.339)
Year2018:In-edge	22.020*** (-6.41)	10.074*** (-2.847)
Year2018:Out-edge	10.88 (-6.437)	5.796* (-2.859)
Year2018:Out-far	8.279 (-5.444)	5.108* (-2.418)
MPAScorpion:In-edge	10.106 (-7.293)	3.754 (-3.24)
MPAScorpion:Out-edge	12.993 (-6.747)	5.125 (-2.997)
MPAScorpion:Out-far	18.654* (-7.732)	8.594* (-3.435)
Soak:Year2018:MPAScorpion	5.123 (-2.873)	1.726 (-1.276)
Soak:Year2018:In-edge	-13.030*** (-3.005)	-5.719*** (-1.335)
Soak:Year2018:Out-edge	-10.328*** (-2.798)	-3.977** (-1.243)
Soak:Year2018:Out-far	-10.874*** (-2.165)	-4.584*** (-0.962)
Soak:MPAScorpion:In-edge	-2.152 (-1.528)	-0.958 (-0.679)
Soak:MPAScorpion:Out-edge	-0.902 (-1.397)	-0.283 (-0.62)
Soak:MPAScorpion:Out-far	-1.671 (-1.606)	-0.762 (-0.713)
Year2018:MPAScorpion:In-edge	-20.424 (-10.842)	-9.295 (-4.816)
Year2018:MPAScorpion:Out-edge	-17.155 (-10.078)	-8.093 (-4.477)
Year2018:MPAScorpion:Out-far	-20.982 (-10.701)	-10.714* (-4.753)
Soak:Year2018:MPAScorpion:In-edge	-2.101 (-4.405)	0.492 (-1.957)
Soak:Year2018:MPAScorpion:Out-edge	-4.441 (-4.009)	-1.509 (-1.781)
Soak:Year2018:MPAScorpion:Out-far	-3.024 (-3.968)	-0.468 (-1.762)
Constant	21.427*** (-2.734)	9.009*** (-1.214)
Observations	1,622	1,622
Adjusted R^2	0.502	0.447
Residual Standard Error (df = 1590)	11.04	4.902
Model $F_{(31,1590)}$	53.71	43.21
Model *p*-value	< 0.0001	< 0.0001

*Note: Values in parentheses reflect standard errors unless otherwise noted; *p<0.05;**p<0.01;***p<0.001.*

Table A2. Results from linear and nonlinear model fits (Eq. A.2-A.3) of soak time to weight per trap (lbs; four left columns) and CPUE (# lobsters per trap; four right columns) for 2006-2008 (06-08) and 2018. Models controlled for MPA (Gull = reference) and trap location (In-deep = reference). The better model fit based on Adjusted R^2 and AIC values is highlighted in bold.

	Linear vs. nonlinear soak time models: 2006-08 and 2018							
	Weight per trap (lbs)				CPUE (# of lobsters)			
	Linear, 06-08	**Nonlinear, 06-08**	**Linear, 2018**	Nonlinear, 2018	Linear, 06-08	**Nonlinear, 06-08**	**Linear, 2018**	Nonlinear, 2018
Soak	0.517*	**4.602****	**3.549*****	2.844	0.291**	**2.503*****	**1.618*****	0.381
	(0.200)	**(1.406)**	**(0.782)**	(4.258)	(0.099)	**(0.693)**	**(0.300)**	(1.633)
Soak_squared		**-0.412****		0.179		**-0.223****		0.314
		(0.140)		(1.061)		**(0.069)**		(0.407)
MPA_Scorpion	-4.247***	**-3.387*****	**4.123****	4.129**	-2.166***	**-1.700*****	**2.235*****	2.245***
	(0.849)	**(0.895)**	**(1.275)**	(1.277)	(0.419)	**(0.441)**	**(0.489)**	(0.490)
In-edge	-7.607***	**-7.618*****	**-22.084*****	-22.079***	-2.684***	**-2.690*****	**-7.664*****	-7.655***
	(0.901)	**(0.898)**	**(1.821)**	(1.823)	(0.444)	**(0.442)**	**(0.699)**	(0.699)
Out-edge	-17.744***	**-17.702*****	**-33.515*****	-33.512***	-7.712***	**-7.689*****	**-12.559*****	-12.552***
	(0.905)	**(0.902)**	**(1.671)**	(1.673)	(0.446)	**(0.444)**	**(0.642)**	(0.642)
Out-far	-17.082***	**-17.026*****	**-34.538*****	-34.540***	-7.319***	**-7.288*****	**-12.904*****	-12.907***
	(0.942)	**(0.939)**	**(1.609)**	(1.611)	(0.464)	**(0.462)**	**(0.618)**	(0.618)
Constant	17.957***	**8.726****	**27.996*****	28.583***	7.851***	**2.851**	**10.053*****	11.084***
	(1.157)	**(3.349)**	**(1.801)**	(3.925)	(0.570)	**(1.650)**	**(0.691)**	(1.506)
AIC	7902.57	**7895.93**	**4566.38**	4568.35	6404.84	**6396.41**	**3488.15**	3489.55
Observations	1,059	**1,059**	**563**	563	1,059	**1,059**	**563**	563
Adjusted R^2	0.341	**0.346**	**0.514**	0.513	0.303	**0.309**	**0.50**	0.503
Residual SE (df)	10.06 (1053)	**10.02 (1052)**	**13.87 (557)**	13.88 (556)	4.96 (1053)	**4.94 (1052)**	**5.32 (557)**	5.32 (556)
F (df)	110.7 (5;1053)	**94.37 (6;1052)**	**119.9 (5;557)**	99.75 (6;556)	92.9 (5;1053)	**79.84 (6;1052)**	**115.1 (5;557)**	95.94 (6;556)
Model *p*-value	< 0.0001	**< 0.0001**	**< 0.0001**	< 0.0001	< 0.0001	**< 0.0001**	**< 0.0001**	< 0.0001

*Note: Values in parentheses reflect standard errors unless otherwise noted; *p<0.05;**p<0.01;***p<0.001.*

Appendix A2; Model fits for each year-MPA-location combination

I assessed linear and nonlinear effects of soak time on catch per trap for each year-MPA-trap location combination using Eq. 1 and 2 from the main text:

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster) = \beta_0 + \beta_1 Soak + \varepsilon, \quad \text{(Eq. 1)}$$

and

$$Catch\ per\ trap\ (pounds\ or\ \#\ of\ lobster) = \beta_0 + \beta_1 Soak + \beta_2 (Soak)^2 + \varepsilon. \quad \text{(Eq. 2)}$$

Variable names and explanations are in the main text. Results from each regression model for both CPUE (numbers per trap) and weight (lbs per trap) are presented below. Each year-MPA-trap location combination is presented in Table A11-A12 with mean and standard error catch per trap values before and after standardization.

Table A3. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to CPUE (# lobsters per trap) in 2006-2008 at Gull MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). Significant model fits used to standardize data are highlighted in bold.

	Gull 2006-2008							
	CPUE (# lobsters per trap)							
	In-deep (Eq. 1)	**In-deep (Eq. 2)**	In-edge (Eq. 1)	**In-edge (Eq. 2)**	Out-edge (Eq. 1)	**Out-edge (Eq. 2)**	**Out-far (Eq. 1)**	Out-far (Eq. 2)
Soak	0.118	**11.483****	0.960***	**6.613****	0.089	**1.900*****	**0.245***	-0.088
	(0.420)	**(3.548)**	(0.286)	**(2.348)**	(0.059)	**(0.515)**	**(0.100)**	(0.955)
Soak_squared		**-1.152****		**-0.582***		**-0.183*****		0.034
		(0.357)		**(0.240)**		**(0.052)**		(0.097)
Constant	9.009***	**-16.437***	2.537	**-9.994**	0.664*	**-3.400****	**0.421**	1.164
	(2.027)	**(8.135)**	(1.334)	**(5.333)**	(0.280)	**(1.180)**	**(0.478)**	(2.172)
AIC	1257.43	**1249.15**	1727.58	**1723.69**	758.92	**748.55**	**970.5**	972.38
Observations	178	**178**	263	**263**	226	**226**	**221**	221
Adjusted R^2	-0.005	**0.046**	0.038	**0.055**	0.006	**0.054**	**0.022**	0.018
Residual SE (df)	8.182 (176)	**7.972 (175)**	6.410 (261)	**6.351 (260)**	1.286 (224)	**1.254 (223)**	**2.155 (219)**	2.159 (218)
F (df)	0.079 (1;176)	**5.240 (2;175)**	11.285 (1;261)	**8.689 (2;260)**	2.275 (1;224)	**7.468 (2;223)**	**6.025 (1;219)**	3.062 (2;218)
Model *p*-value	0.78	**0.006**	0.0009	**0.0002**	0.13	**0.0007**	**0.015**	0.049

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A4. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to CPUE (# lobsters per trap) in 2006-2008 at Scorpion MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). There were no significant model fits so no columns are highlighted in bold.

	Scorpion 2006-2008							
	CPUE (# lobsters per trap)							
	In-deep (Eq. 1)	In-deep (Eq. 2)	In-edge (Eq. 1)	In-edge (Eq. 2)	Out-edge (Eq. 1)	Out-edge (Eq. 2)	Out-far (Eq. 1)	Out-far (Eq. 2)
Soak	0.320	2.365	0.204	-0.204	0.007	-0.174	-0.315	-0.484
	(0.349)	(1.821)	(0.208)	(1.120)	(0.047)	(0.259)	(0.215)	(1.024)
Soak_squared		-0.199		0.040		0.018		0.017
		(0.174)		(0.108)		(0.025)		(0.103)
Constant	3.708*	-0.710	0.990	1.851	0.488*	0.874	3.715**	4.044
	(1.674)	(4.206)	(0.992)	(2.535)	(0.235)	(0.591)	(1.038)	(2.216)
AIC	199	199.6	187.89	189.74	176.21	177.68	121.67	123.64
Observations	35	35	39	39	71	71	26	26
Adjusted R^2	-0.005	0.005	-0.001	-0.025	-0.014	-0.021	0.044	0.004
Residual SE (df)	3.926 (33)	3.908 (32)	2.558 (37)	2.588 (36)	0.814 (69)	0.817 (68)	2.329 (24)	2.378 (23)
F (df)	0.838 (1;33)	1.077 (2;32)	0.954 (1;37)	0.534 (2;36)	0.024 (1;69)	0.266 (2;68)	2.154 (1;24)	1.048 (2;23)
Model *p*-value	0.367	0.353	0.335	0.591	0.876	0.767	0.1552	0.367

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A5. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to CPUE (# lobsters per trap) in 2018 at Gull MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). Significant model fits used to standardize data are highlighted in bold.

	Gull 2018							
	CPUE (# lobsters per trap)							
	In-deep (Eq. 1)	In-deep (Eq. 2)	In-edge (Eq. 1)	In-edge (Eq. 2)	Out-edge (Eq. 1)	Out-edge (Eq. 2)	Out-far (Eq. 1)	Out-far (Eq. 2)
Soak	**4.384*****	4.201	-0.493	16.320	0.379	-1.250	-0.073	0.332
	(0.712)	(3.249)	(2.458)	(13.949)	(0.392)	(2.452)	(0.080)	(0.428)
Soak_squared		0.046		-4.537		0.418		-0.100
		(0.790)		(3.706)		(0.621)		(0.104)
Constant	**3.973****	4.129	7.575	-5.727	1.424	2.765	0.494**	0.147
	(1.348)	(3.013)	(4.447)	(11.730)	(0.785)	(2.143)	(0.165)	(0.397)
AIC	**707.11**	709.1	306.7	307.11	168.19	169.7	173.53	174.58
Observations	**112**	112	40	40	40	40	93	93
Adjusted R^2	**0.250**	0.243	-0.025	-0.012	-0.002	-0.016	-0.002	-0.003
Residual SE (df)	**5.585 (110)**	5.610 (109)	10.649 (38)	10.579 (37)	1.885 (38)	1.899 (37)	0.602 (91)	0.602 (90)
F (df)	**37.903 (1;110)**	18.781 (2;109)	0.040 (1;38)	0.770 (2;37)	0.933 (1;38)	0.686 (2;37)	0.833 (1;91)	0.879 (2;90)
Model *p*-value	**< 0.0001**	< 0.0001	0.842	0.470	0.340	0.510	0.364	0.419

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001.*

Table A6. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to CPUE (# lobsters per trap) in 2018 at Scorpion MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). Significant model fits used to standardize data are highlighted in bold.

	Scorpion 2018							
	CPUE (# lobsters per trap)							
	In-deep (Eq. 1)	In-deep (Eq. 2)	In-edge (Eq. 1)	**In-edge (Eq. 2)**	Out-edge (Eq. 1)	Out-edge (Eq. 2)	Out-far (Eq. 1)	Out-far (Eq. 2)
Soak	**6.312*****	7.639	0.969	**-9.816***	0.514	-3.151	0.626	-2.374
	(1.731)	(10.710)	(0.796)	**(4.610)**	(0.353)	(2.050)	(0.414)	(2.550)
Soak_squared		-0.339		**2.732***		0.949		0.755
		(2.699)		**(1.151)**		(0.523)		(0.633)
Constant	**6.737**	5.633	4.798**	**13.926****	1.220	4.247*	1.138	3.681
	(3.511)	(9.483)	(1.650)	**(4.162)**	(0.696)	(1.806)	(0.871)	(2.303)
AIC	**310.56**	312.54	363.9	**360.25**	604.61	603.28	236.52	237.03
Observations	**43**	43	61	**61**	122	122	52	52
Adjusted R^2	**0.227**	0.208	0.008	**0.080**	0.009	0.028	0.025	0.033
Residual SE (df)	**8.553 (41)**	8.657 (40)	4.624 (59)	**4.453 (58)**	2.837 (120)	2.810 (119)	2.264 (50)	2.255 (49)
F (df)	**13.302 (1;41)**	6.499 (2;40)	1.481 (1;59)	**3.614 (2;58)**	2.126 (1;120)	2.730 (2;119)	2.287 (1;50)	1.864 (2;49)
Model *p*-value	**0.0007**	0.004	0.229	**0.033**	0.147	0.069	0.137	0.166

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A7. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to weight per trap (lbs) in 2006-2008 at Gull MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). Significant model fits used to standardize data are highlighted in bold.

	Gull 2006-08							
	Weight per trap (lbs)							
	In-deep (Eq. 1)	**In-deep (Eq. 2)**	In-edge (Eq. 1)	**In-edge (Eq. 2)**	Out-edge (Eq. 1)	**Out-edge (Eq. 2)**	**Out-far (Eq. 1)**	Out-far (Eq. 2)
Soak	-0.045	**21.378****	1.875***	**12.868****	0.152	**2.812****	**0.376***	-0.297
	(0.905)	**(7.692)**	(0.543)	**(4.459)**	(0.096)	**(0.845)**	**(0.178)**	(1.699)
Soak_squared		**-2.172****		**-1.131***		**-0.269****		0.068
		(0.774)		**(0.455)**		**(0.085)**		(0.172)
Constant	21.427***	**-26.541**	4.932	**-19.436**	1.030*	**-4.942***	**0.903**	2.403
	(4.363)	**(17.635)**	(2.535)	**(10.128)**	(0.457)	**(1.937)**	**(0.850)**	(3.865)
AIC	1530.41	**1524.59**	2065.25	**2061.08**	980.68	**972.73**	**1225.22**	1227.06
Observations	178	**178**	263	**263**	226	**226**	**221**	221
Adjusted R^2	-0.006	**0.032**	0.040	**0.059**	0.007	**0.045**	**0.016**	0.012
Residual SE (df)	17.615 (176)	**17.281 (175)**	12.180 (261)	**12.061 (260)**	2.100 (224)	**2.059 (223)**	**3.834 (219)**	3.842 (218)
F (df)	0.002 (1;176)	**3.932 (2;175)**	11.932 (1;261)	**9.168 (2;260)**	2.473 (1;224)	**6.308 (2;223)**	**4.475 (1;219)**	2.308 (2;218)
Model *p*-value	0.961	**0.021**	0.0006	**0.0001**	0.117	**0.002**	**0.0355**	0.102

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A8. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to weight per trap (lbs) in 2006-2008 at Scorpion MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). There were no significant model fits so no columns are highlighted in bold.

	Scorpion 2006-08							
	Weight per trap (lbs)							
	In-deep (Eq. 1)	In-deep (Eq. 2)	In-edge (Eq. 1)	In-edge (Eq. 2)	Out-edge (Eq. 1)	Out-edge (Eq. 2)	Out-far (Eq. 1)	Out-far (Eq. 2)
Soak	0.713	5.222	0.481	-1.128	0.007	-0.326	-0.538	-0.488
	(0.809)	(4.227)	(0.451)	(2.412)	(0.091)	(0.501)	(0.415)	(1.982)
Soak_squared		-0.440		0.158		0.032		-0.005
		(0.405)		(0.232)		(0.048)		(0.198)
Constant	8.344*	-1.396	1.955	5.361	0.940*	1.651	6.474**	6.377
	(3.878)	(9.763)	(2.145)	(5.458)	(0.454)	(1.144)	(2.009)	(4.290)
AIC	257.81	258.55	248.06	249.56	269.87	271.39	156	158
Observations	35	35	39	39	71	71	26	26
Adjusted R^2	-0.007	-0.001	0.004	-0.011	-0.014	-0.022	0.026	-0.016
Residual SE (df)	9.096 (33)	9.071 (32)	5.533 (37)	5.574 (36)	1.574 (69)	1.580 (68)	4.507 (24)	4.604 (23)
F (df)	0.777 (1;33)	0.981 (2;32)	1.138 (1;37)	0.792 (2;36)	0.007 (1;69)	0.233 (2;68)	1.680 (1;24)	0.805 (2;23)
Model *p*-value	0.385	0.386	0.293	0.461	0.936	0.793	0.207	0.459

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A9. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to weight per trap (lbs) in 2018 at Gull MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). Significant model fits used to standardize data are highlighted in bold.

	Gull 2018							
	Weight per trap (lbs)							
	In-deep (Eq. 1)	In-deep (Eq. 2)	In-edge (Eq. 1)	In-edge (Eq. 2)	Out-edge (Eq. 1)	Out-edge (Eq. 2)	Out-far (Eq. 1)	Out-far (Eq. 2)
Soak	**10.316*****	9.211	-0.794	48.961	0.184	-4.747	-0.138	0.425
	(1.985)	(9.055)	(6.284)	(35.418)	(0.796)	(4.938)	(0.125)	(0.671)
Soak_squared		0.275		-13.427		1.266		-0.139
		(2.201)		(9.410)		(1.251)		(0.163)
Constant	**13.045*****	13.984	18.571	-20.797	3.529*	7.588	0.801**	0.317
	(3.756)	(8.396)	(11.371)	(29.785)	(1.592)	(4.316)	(0.258)	(0.622)
AIC	**936.7**	938.68	381.8	381.66	224.8	225.71	256.92	258.17
Observations	**112**	112	40	40	40	40	93	93
Adjusted R^2	**0.190**	0.183	-0.026	0.001	-0.025	-0.024	0.002	-0.001
Residual SE (df)	**15.564 (110)**	15.634 (109)	27.227 (38)	26.863 (37)	3.826 (38)	3.825 (37)	0.943 (91)	0.944 (90)
F (df)	**27.013 (1;110)**	13.393 (2;109)	0.016 (1;38)	1.026 (2;37)	0.053 (1;38)	0.539 (2;37)	1.222 (1;91)	0.974 (2;90)
Model *p*-value	**< 0.0001**	<0.0001	0.900	0.368	0.818	0.588	0.272	0.382

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A10. Results from linear (Eq. 1) and nonlinear (Eq. 2) model fits of soak time to weight per trap (lbs) in 2018 at Scorpion MPA for every trap location category (In-deep, In-edge, Out-edge, Out-far). Significant model fits used to standardize data are highlighted in bold.

	Scorpion 2018							
	Weight per trap (lbs)							
	In-deep (Eq. 1)	In-deep (Eq. 2)	In-edge (Eq. 1)	**In-edge (Eq. 2)**	Out-edge (Eq. 1)	Out-edge (Eq. 2)	Out-far (Eq. 1)	Out-far (Eq. 2)
Soak	**16.197****	43.815	0.833	**-25.496****	0.722	-5.468	1.048	-3.815
	(5.057)	(30.988)	(1.672)	**(9.513)**	(0.729)	(4.257)	(0.749)	(4.626)
Soak_squared		-7.056		**6.670****		1.602		1.224
		(7.810)		**(2.376)**		(1.086)		(1.149)
Constant	**16.549**	-6.433	11.757**	**34.042*****	2.870*	7.983*	1.976	6.099
	(10.261)	(27.438)	(3.465)	**(8.590)**	(1.440)	(3.750)	(1.575)	(4.178)
AIC	**402.77**	403.91	454.42	**448.65**	781.82	781.61	298.19	298.99
Observations	**43**	43	61	**61**	122	122	52	52
Adjusted R^2	**0.181**	0.177	-0.013	**0.093**	-0.0002	0.010	0.018	0.021
Residual SE (df)	24.991 (41)	25.048 (40)	9.711 (59)	9.190 (58)	5.865 (120)	5.836 (119)	4.097 (50)	4.091 (49)
F (df)	10.256 (1;41)	5.513 (2;40)	0.249 (1;59)	4.078 (2;58)	0.980 (1;120)	1.583 (2;119)	1.957 (1;50)	1.548 (2;49)
Model *p*-value	**0.003**	0.008	0.620	**0.022**	0.324	0.210	0.168	0.223

*Note: Values in parentheses reflect standard errors; *p<0.05;**p<0.01;***p<0.001*

Table A11. CPUE values (# lobsters per trap) before (raw data) and after standardization for soak time (adjusted) for each combination of MPA, Year, and Trap Location. The "Adjust?" column indicates whether data was standardized for a given site/year, and the % Change column indicates how much mean CPUE increased or decreased following standardization. Site data that were standardized are highlighted in bold text.

MPA	Year	Trap Location	Mean CPUE, raw data	Raw SE	Mean CPUE, adjusted	Adjusted SE	Adjust? (Y/N)	% Change
Gull	**06-08**	**In-deep**	**9.55**	**0.61**	**7.65**	**0.46**	**Y**	**-19.95%**
Scorpion	06-08	In-deep	5.11	0.66	5.11	0.66	N	0.00%
Gull	**2018**	**In-deep**	**11.61**	**0.61**	**17.15**	**0.76**	**Y**	**47.74%**
Scorpion	**2018**	**In-deep**	**18.63**	**1.48**	**25.66**	**1.69**	**Y**	**37.76%**
Gull	**06-08**	**In-edge**	**6.82**	**0.40**	**4.62**	**0.25**	**Y**	**-32.25%**
Scorpion	06-08	In-edge	1.87	0.41	1.87	0.41	N	0.00%
Gull	2018	In-edge	6.75	1.66	6.75	1.66	N	0.00%
Scorpion	**2018**	**In-edge**	**6.67**	**0.59**	**9.07**	**0.78**	**Y**	**35.89%**
Gull	**06-08**	**Out-edge**	**1.07**	**0.09**	**0.66**	**0.05**	**Y**	**-38.37%**
Scorpion	06-08	Out-edge	0.52	0.10	0.52	0.10	N	0.00%
Gull	2018	Out-edge	2.13	0.30	2.13	0.30	N	0.00%
Scorpion	2018	Out-edge	2.16	0.26	2.16	0.26	N	0.00%
Gull	**06-08**	**Out-far**	**1.54**	**0.15**	**1.16**	**0.11**	**Y**	**-24.85%**
Scorpion	06-08	Out-far	2.35	0.47	2.35	0.47	N	0.00%
Gull	2018	Out-far	0.35	0.06	0.35	0.06	N	0.00%
Scorpion	2018	Out-far	2.37	0.32	2.37	0.32	N	0.00%

Table A12. Weight (wt) per trap values (lbs) before (raw data) and after standardization for soak time (adjusted) for each combination of MPA, Year, and Trap Location. The "Adjust?" column indicates whether data was standardized for a given site/year, and the % Change column indicates how much mean weight per trap increased or decreased following standardization. Site data that were standardized are highlighted in bold text.

MPA	Year	Trap Location	Mean wt per trap, raw data	Raw SE	Mean wt per trap, adjusted	Adjusted SE	Adjust? (Y/N)	% Change
Gull	**06-08**	**In-deep**	**21.22**	**1.32**	**18.06**	**1.07**	**Y**	**-14.91%**
Scorpion	06-08	In-deep	11.48	1.53	11.48	1.53	N	0.00%
Gull	**2018**	**In-deep**	**31.01**	**1.63**	**44.04**	**1.99**	**Y**	**42.05%**
Scorpion	**2018**	**In-deep**	**47.06**	**4.21**	**64.86**	**5.02**	**Y**	**37.83%**
Gull	**06-08**	**In-edge**	**13.30**	**0.77**	**9.01**	**0.49**	**Y**	**-32.22%**
Scorpion	06-08	In-edge	4.04	0.89	4.04	0.89	N	0.00%
Gull	2018	In-edge	17.24	4.25	17.24	4.25	N	0.00%
Scorpion	**2018**	**In-edge**	**13.37**	**1.24**	**17.58**	**1.56**	**Y**	**31.52%**
Gull	**06-08**	**Out-edge**	**1.71**	**0.14**	**1.08**	**0.09**	**Y**	**-36.97%**
Scorpion	06-08	Out-edge	0.97	0.19	0.97	0.19	N	0.00%
Gull	2018	Out-edge	3.87	0.60	3.87	0.60	N	0.00%
Scorpion	2018	Out-edge	4.19	0.53	4.19	0.53	N	0.00%
Gull	**06-08**	**Out-far**	**2.62**	**0.26**	**2.03**	**0.20**	**Y**	**-22.36%**
Scorpion	06-08	Out-far	4.14	0.90	4.14	0.90	N	0.00%
Gull	2018	Out-far	0.54	0.10	0.54	0.10	N	0.00%
Scorpion	2018	Out-far	4.03	0.57	4.03	0.57	N	0.00%

Appendix A References

Hlavac, Marek (2018). stargazer: Well-Formatted Regression and Summary Statistics Tables.
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